A CYTOTAXONOMIC INVESTIGATION ON

THE ASPLENIUM AETHIOPICUM COMPLEX IN AFRICA.

A Thesis submitted to the University of Leeds

for the Degree of

Doctor of Philosophy

by

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November 1964.

CONTENTS.

GENERAL INTRODUCTION.

The present investigation arose through some preliminary work on Asplenium aethiopicum (Burm) Bech. in Africa by Professor Manton and Panigrahi (Thesis 1954). This work showed it to be a complex of a highly polyploid character with at least three cytological types; and these features coupled with considerable morphological variation long recognised by taxonomists but defying satisfactory treatment by conventional taxonomic methods, suggested the complex as a suitable subject for cytotaxonomic studies.

Although in the intervening years since the earlier studies further material had been accumulated, it was recognised at the outset that the problem could not be undertaken seriously without fieldwork in Africa and also some initial guidance on the taxonomic aspects from an expert on African ferns. These requirements were fulfilled by the opportune visit to this country in 1959 by Dr. E.A. Schelpe, Curator of the Bolus Herbarium, University of Cape Town, who co-operated with Professor Manton in giving some taxonomic guidance and agreeing to supervise and assist the author during fieldwork in South Africa. It was therefore possible through financial support and co-operation of the D.S.I.R., the British Council and the University of Leeds to spend the year July 1960 to July 1961 collecting material and data in South Africa, northern Tanganyika and Kenya.

In preparation for fieldwork in Africa a morphological survey of the material in the national herbaria in London was undertaken. From this it was soon evident that a number of other species were

frequently being confused both with the A. aethiopicum complex and with each other, which made it necessary to include them in these studies. Most of these ill-defined species have been typified and satisfactorily separated from the complex but some have subsequently been shown to be made up of more than one cytotype. These additional cytotypes were first detected during the herbarium studies as were further morphological and cytological forms within A. aethiopicum and their localities were noted for future fieldwork. While it was possible to visit several of these important localities and collect plants personally; plants or spores were gathered from others through the generous response of correspondents.

The incorporation of much new material into the research programme after returning from Africa has meant that the investigation has enlarged considerably beyond the scope originally envisaged. In consequence the bulk of the data accumulated makes it necessary to restrict the detailed presentation in this thesis to the A. aethiopicum complex. The other species referred to in the last paragraph will be listed in a brief Appendix. This will include their chromosome numbers and although brief will serve to show which species in addition to the A. aethiopicum complex are under investigation as well as a record of the levels of polyploidy in species sometimes confused with the complex in Africa.

The aim of the present investigation has been to show the nature of the cytological and genetical relationships existing between the different cytotypes making up the complex and also between the morphological forms within each cytotype, to provide a basis for

determining their taxonomic status. Apart from the taxonomic implications of much of the data accumulated it was felt this would also contribute to the wider and very relevant questions of evolutionary mechanisms operating in ferns, particularly in a group with an apparently very highly developed polyploid series.

The procedures adopted during the course of the work are those usual in an investigation of this nature. These include the morphological studies already mentioned, cytological sampling and study of ecological and distribution data of the different cytotypes, which take up a considerable part of the main body of this thesis. After an introduction to the complex (chap. II) a lengthy section (chap. III) is devoted to the morphology, ecology and distribution of the sexual cytotypes. The morphological treatment is set against the present taxonomic background in the hope that it will provide a clearer illustratic of the taxonomic problems involved and show at the same time the extent of morphological variation in the complex.

The cytogenetic procedures have consisted broadly of the artificial synthesis in a large breeding programme of both interploidal and intra-ploidal hybrids and the study of chromosome pairing at meiosis in these as well as wild hybrids, as a source of information concerning the cytological relationships of the sexual cytotypes. These aspects are dealt with in chapters IV and V.

As data became available new problems unforseen at the outset emerged; one of the most important and rewarding being the hitherto unknown apogamous section of the complex. These apomicts have been encountered with sufficient frequency to justify their treatment in a

separate section (chap. VI). Their sporangial development is also summarised in the same chapter since this is of an interesting and unusual type encountered here for the first time in apogamous Pteridophyta.

The illustrations have been separated from the text and are placed together at the back of the thesis in the belief that this will make reference to them easier and avoids breaking up the text. In the text reference is frequently made to plants by the collector's name and number. For personal collections this has been abbreviated to the letter B which precedes the number of the gathering.

I. MATERIALS AND METHODS.

1. MATERIALS.

a) Live plants.

At the outset of the investigation two cytotypes of A.aethiopicum were still in cultivation from Panigrahi's earlier work. In addition six further plants had been accumulated over a number of years by Professor Manton either as live specimens sent by correspondents in Africa or by raising plants from spores taken from herbarium sheets.

The majority of plants studied during the investigation were obtained through fieldwork in South Africa, Northern Tanganyika and Kenya. These have been supplemented by raising plants from spores taken from herbarium sheets in the National Herbaria in London and the Bolus Herbarium, Cape Town, and by plants collected by Dr. E.A. Schelpe and other collectors in Africa. A considerable quantity of living material therefore has been available, consisting of some 70 plants representing the different cytotypes and natural hybrids of the A. aethiopicum complex and a further 25 plants representing other species and their cytotypes referred to in the General Introduction.

b) Herbarium material.

Herbarium material has been made available for study by the British Museum and Kew Herbaria in London and all the major herbaria in southern Africa. In addition a large quantity of personal material was accumulated during fieldwork in Africa.

2. METHODS.

The methods employed in an investigation of this nature at Leeds are now to a large extent standard. Nevertheless each new investigation raises its own difficulties or peculiarities which require modification of technique. In dealing with the methods, therefore, detail will be limited to these modifications and other features of interest, and the reader will be referred to earlier investigations for details of more standard techniques.

a) Collection and transport of wild plants.

Material collected from localities in South Africa was initially established in cultivation at the National Botanic Gardens, Kirstenbosch. It was later packed as outlined in Manton and Sledge (1954) and transported by air to Kew. Plants gathered in N. Tanganyika and Kenya were packed in a similar manner in the field and sent direct to Kew. Most of the material was finally transferred to Leeds in the summer of 1962.

Loss of plants was experienced after each transfer, but the effect of these losses was minimised by keeping a reserve of duplicates of important specimens, and by ensuring that viable spores were collected from each plant before transfer so that in the event of total loss new plants could be raised. The majority of the plants withstood the transfer very well and actual losses sustained were reasonably low.

b) Horticultural Methods.

The preparation of pots, soil mixtures, etc. are described by previous investigators and need not be repeated here.

i) Spores and Prothalli.

Pots sown with spores normally appear green after 2 - 5 weeks in

a closed frame at 55° - 65° F. Subsequent growth is relatively slow and antheridia are not produced until $2\frac{1}{2}$ - $3\frac{1}{2}$ months after sowing, at which time most of the prothalli will yield swimming spermatozoids when immersed in water for 5 - 10 minutes. The archegonia generally appear about a month after the first antheridia.

After 4 - 5 months have elapsed from sowing it is usually possible to determine the breeding system of the prothalli. If it is evident that the prothalli are sexual and young sporelings are required, the culture is flooded with water to effect fertilisation and if this has been successful young sporelings begin to appear a month later. In the case of apogamous prothalli no fertilisation is necessary and the apogamous outgrowths giving rise to the first leaves generally become obvious $4\frac{1}{2}$ - $5\frac{1}{2}$ months after sowing the spores.

Apogamous prothalli cultured so far have shown very poor antheridial production. On immersing these prothalli in water to obtain swimming spermatozoids for hybridisation experiments only occasional very sluggish spermatozoids have been observed. This behaviour contrasts strongly with the situation in other apogamous ferns where prothalli produce abundant antheridia, which readily yield swimming spermatozoids (Manton, 1950; Walker, 1958). The culture conditions were modified slightly to try and improve antheridial production and potential swimming capacity of the spermatozoids. Pots containing prothalli were kept dry just before the time at which antherida formation was expected. Pots were also transferred to a slightly cooler frame. Neither of these modifications effected any substantial improvement in the swimming capacity of the spermatozoids though the latter perhaps resulted in a slight increase in the numbers of antheridia. The paucity of antheridia

and the inability to produce swimming spermatozoids may be due to unsuitable horticultural procedures, but the possibility of these features being inherent characteristics of the prothalli cannot be ignored.

The prothallial cultures, both sexual and apogamous, were susceptible to a number of pests but these did not seriously interfere with the research programme. These pests and any preventive measures or cures are adequately dealt with by Walker (Thesis, 1956).

ii) Hybridisation.

The techniques used for hybridisation in ferns have been adequately described by previous workers in Leeds.

If the hybridisation attempt is successful young sporophytes appear 4 - 6 weeks after insemination.

Some of the prothalli cultured produce antheridia over a fairly lengthy period of up to two or more months, which has certain advantages regarding availability of spermatozoids for hybridisation experiments. It also means, however, that there is a considerable overlap, as in many fern prothalli, of the antheridial and archegonial phases of development. If possible, therefore, 'female prothalli' were not used for hybridisation until six or more months old even though archegonia may first have appeared $3\frac{1}{2}$ - $4\frac{1}{2}$ months after sowing. The prothalli then have few, if any, antheridia and abundant archegonia thus increasing the chances of fertilisation by a spermatozoid of the selected male parent as opposed to self-fertilisation.

It has been generally impracticable to determine the hybridity of young sporophytes by root tip squash methods, because of the high

chromosome numbers involved, and also because these methods are potentially uninformative for a considerable number of hybrids synthesised between parents with the same chromosome number. Normally in such cases it would be necessary to wait until the plants reached morphological maturity or underwent meiosis before being sure that hybrids had been produced. However space considerations precluded the growing of large numbers of plants of any one cross to maturity, and it was therefore necessary to be reasonably certain that sporelings arising from prothalli after hybridisation were hybrids and not the result of self-fertilisation.

No other special techniques were used to prevent self-fertilisation of prothalli (e.g. Walker, Thesis, 1956) as these did not appear to be completely successful and were time consuming, but the use of 'mature prothalli' as female parent has kept self-fertilisation to a low level in the hybridisation programme. Evidence for this was often seen in attempts to synthesise hybrids between A. aethiopicum (as female) and other presumably distantly related species, where no sporophytes emerged showing the absence of both fertilisation by the male parent and self-fertilisation.

iii) Sporophytes.

Young sporophytes were grown in shaded greenhouses at temperatures ranging from 60° - 75° F. Growth is most vigorous in spring and autumn which may be expected for sub tropical plants in this country, when their day length requirement is considered. The time required for the young plants to produce fronds bearing sori varies considerably but is most commonly one to two years, although a number of plants do take longer.

Both young and mature sporophytes, in common with other ferns, are very susceptible to attack by scale insects. Effective control of these damaging insects is difficult and they appear to be almost impossible to eliminate completely. The pest however can be kept at a reasonably low and ineffective level by first scraping badly infested fronds to dislodge the insects, and then dipping the whole plant in a product known commercially as "Volk".

c) Cytology.

The chromosome numbers of the plants under investigation are high, ranging from 2n = 144 to 2n = 432. To obtain accurate counts from cells with chromosome numbers of this order is difficult in the genus Asplenium using root tip squash methods and can be very time consuming. For this reason, and as most plants produce sporangia in cultivation without difficulty, almost exclusive reliance has been made on acetocarmine meiotic squash preparations from sporangia for routine chromosome counts.

i) Acetocarmine sporangial squashes.

(see Manton, 1950).

ii) Sporangial sections.

These sections were used to determine the sporangial development (including the course of meiosis) in the apogamous forms within the complex. After carefully removing the indusium whole sori were cut out from the pinnae. The sori were then fixed either in full strength chromo-acetic formalin or 2BD, embedded in paraffin wax, sectioned at 8 or 10μ and stained in Heidenhain's haematoxylin.

(for details see Manton, 1950).

iii) Chromosome analysis in hybrids.

The analysis of chromosome pairing in the hybrids is beset by a number of difficulties arising principally from their high chromosome numbers coupled with the presence in many cases of both univalents and paired groups, some of the latter being multivalent. Analysis of such cells is a much more difficult problem than analysis of cells with a similar number of chromosomes, but where they all appear as either univalents or bivalents, and usually requires better cells, squashed so that the chromosomes are well separated. To obtain cells of this quality has not been easy partly because of their high chromosome numbers, but also because the mere presence of multivalents in many hybrids appears to increase the difficulties of squashing cells effectively. For these reasons it has frequently been necessary to fix sporangia from a plant several times before even one cell suitable for analysis is obtained, and consequently the number of cells analysed in detail for any one hybrid combination ~~are~~ is small.

It has not usually been possible to determine the number and nature of multivalents accurately but this will be further discussed in the chapter on artificial hybrids.

In certain hybrid combinations the number of chromosomes pairing at meiosis varies considerably in the same plant. In one tetraploid hybrid an extreme case was seen in which the first meiotic preparations showed complete failure of pairing while in later preparations pairing was complete. In this case there does appear to be a relationship between the amount of pairing and age of the plant (see p.63). In other cases, however, the evidence is less certain and the variation may be attributable to metabolic causes of a similar nature to those

suggested by Manton and Sledge (1954) when occasional failure of chromosome pairing was noted during summer for tropical ferns cultivated in this country. It has therefore been desirable to obtain analysable cells from the same plant at least twice, if possible at different times of the year, in order to check the chromosome behaviour.

d) Spores.

i) Collection.

Spores were collected in greaseproof paper packets and to ensure purity of samples the precautions described by previous investigators were followed.

ii) Spore mounts.

Spores were mounted in gum chloral which is particularly convenient to use in herbaria. These mounts were suitable for measuring spores and to ensure consistency in mounting of spores for this purpose, no other method has been employed.

iii) Measurements.

Spores were measured using a calibrated micrometer eyepiece and a X40 objective.

e) Photographic techmiques.

i) Silhouettes of fronds.

(see Manton, 1950).

ii) Chromosome photography and diagrams.

a) Acetocarmine squash preparations.

These were photographed at a magnification of a 1000 times on Ilford Special Rapid Panchromatic Plates using a x 100 Watson oil objective and green filter, but where additional contrast was required Ilford Rapid Process Panchromatic Plates were used. A few larger cells

were photographed at magnifications of either x 500 or x 750 using a x 45 fluorite oil objective (Cooke Yellow Band) and on printing enlarged to 1000 diameters. Except for the latter all photographs reproduced are contact prints.

The chromosome diagrams were prepared as outlined in Manton, 1950.

b) Sporangial sections.

Whole sporangia were photographed at a magnification of x 500 on Ilford Special Rapid Panchromatic Plates using a x 45 fluorite oil objective (Cooke Yellow Band). Photomicrographs of detail from the sporangia were taken on the same plates at a magnification of x 1000 and using a x 100 Watson oil objective.

iii) Rhizome scale drawings.

Scales were mounted and projected at a magnification of x 60 onto matt photographic paper. The print was then used as a basis for an ink drawing in the same way as for the chromosome diagrams (see Manton, 1950).

iv) Spores.

Spores were photographed at a magnification of 200 times using a x 10 eyepiece and x 25 objective.

II. INTRODUCTION TO THE COMPLEX.

Recently the name A. aethiopicum (Burm) Bech. has been most commonly applied to a large group of subtropical ferns in Africa, although ferns with almost identical facies are known from Ceylon, S. India, S.E. Asia, Australia, Central and South America and some of the Caribbean Islands. The present investigation is concerned only with representatives of the complex from Africa and the offshore Atlantic Islands.

The complex has masqueraded under other specific epithets in the past, and as these are the only ones evident in some herbaria it will be profitable to give a brief taxonomic history in as far as the name A. aethiopicum is concerned.

The 'species' was first described as Trichomanes aethiopicum by Burmann in 1768 using material from the Cape, S. Africa. Later in 1788 Swartz named rather similar material from Jamaica as A. praemorsum and in 1800 Thunberg described A. furcatum based on further material from the Cape. During the 19th Century the resemblance between A. furcatum Thunb. and A. praemorsum Sw. was noted but the treatment of the African material by various taxonomists differed. Some placed the material under A. furcatum while others placed it under A. praemorsum with A. furcatum as a synonym. The trend towards the reduction of A. furcatum to synonymy beneath the earlier A. praemorsum was probably established by the appearance of Kuhn's Filicales Africanae in 1868. Sim (1892), however, did not follow Kuhn in this respect when he put the S. African material under A. furcatum in the first edition of his "The Ferns of South Africa" but this material was placed under A. praemorsum in the

second edition in 1915.

Kuhn, in common with the earlier taxonomists, was apparently unaware of the species described by Burmann or if aware did not recognise it as being similar to either A. furcatum or A. praemorsum. In 1935 Becherer saw a close resemblance between Trichomanes aethiopicum and A. praemorsum Sw. and on rules of priority constituted the new combination of Asplenium aethiopicum, listing 9 synonyms including A. praemorsum and A. furcatum. This new combination has since been widely recognised, being used in all recent publications on the fern flora of Africa. (Alston, 1944; Alston, 1959; Alston and Schelpe, 1952; Hedberg, 1957; Cufodontis, 1952; Harley, 1955)

The number of synonyms listed by Becherer (1935) and the even larger number cited by Kuhn (1868) reflects to some extent the complex taxonomic history of the group. They also show long recognition by taxonomists of the apparent morphological continuity within the complex and illustrate vividly the difficulties experienced by them in defining any satisfactory morphological barriers delimiting good species.

It is relatively more recently that the cytological complexity of A. aethiopicum has emerged, mainly through work by Professor Manton and colleagues as explained in the General Introduction. The complex is highly polyploid, the three cytotypes used by Manton and Panigrahi having had 72, 144 and 216 chromosomes at meiosis. Since the monoploid chromosome number in the genus Asplenium is 36 (Manton, 1950) the levels of ploidy represented by these chromosome numbers are tetraploid, octoploid and dodecaploid (12 ploid) respectively.

In the present investigation the three levels of ploidy mentioned above have been the most frequently encountered in the complex and an

example of each is illustrated in figs. 1, 2 and 3. In addition, however, two decaploid plants are now known from S. Africa which are part of the previously unknown and otherwise octoploid apogamous section of the complex.

In attempting to define the complex in morphological terms one encounters difficulties of a similar nature to those mentioned by Copeland (1947) when he refers to "natural groups" in the genus Asplenium as being "remarkably undefinable". It is difficult to detect any one tangible character which would certainly place a specimen in the complex. Nevertheless to quote Hooker (Sp.Fil.III) writing on A. furcatum Thunb. "Varying as this extensively diffused species assuredly is in its composition, more or less divided, and in the apices of the pinnae and pinnules more or less truncated or acuminated, yet it is in most cases easily recognised. In India, however, there are ....".

For the material used in this thesis and in agreement with the views of Hooker, the members of the A. aethiopicum complex are generally easily recognised from those of related complexes or species and their separation from these may be effected by means of the following series of characters:

i) Rhizome creeping, but never long creeping with widely spaced fronds, so that fronds usually tufted or semi-tufted at the growing point.

ii) Rhizome scales 3 - 10 mm. long and narrow, rarely more than 1.5 mm. wide at the base.

iii) Fronds bipinnatifid to quadripinnatifid and clothed sparsely to densely with reddish-brown to dark brown

scales with long hair points or fibrils, particularly on the base of the stipe, rachis and undersurface of the pinnae.

iv) Pinnae always longer than broad, subopposite and divided into alternate pinnules and, or lobes.

v) Pinnules subflabellate, cuneate and the larger ones alternately divided into further lobes.

vi) Ultimate lobes with apical margins irregularly serrate or more deeply incised into often irregular furcate teeth, producing a jagged (praemorsum) appearance.

Within the complex, delimitation of useful subsections is a much more difficult problem. The herbarium survey, mentioned in the General Introduction, during the course of which nearly two thousand specimens were examined, revealed only a few potentially useful characters, many being of a rather subtle nature and consequently difficult to define for comparative purposes. A survey of the literature showed a similar situation since special emphasis has not usually been laid on any one type of character although those most frequently used include degree of dissection of the frond, pinnule shape and structure of the rhizome scales. This lack of emphasis and the short list of characters is perhaps a true indication of the difficulty of finding tangible features for effective separation of taxa within the complex. Nevertheless some personal comments on the various characters potentially available for this purpose may perhaps be usefully given as follows:

i) Rhizome.

All forms possess rhizomes which creep to a greater or lesser extent producing fronds which are either tufted or semi-tufted at

the growing point. It has not been possible to detect any marked discontinuities in this feature though there are certain tendencies correlated with the level of ploidy, and sometimes with the degree of dissection at the tetraploid level, which will emerge in the more detailed morphological treatment in the next chapter. It may be noted here that once plants are in cultivation their rhizomes may not behave as in the wild, since a reduction in their ability to creep has been observed in some instances.

ii) Rhizome scales.

These are always clathrate with some differences in length and breadth, colour, size of constituent cells, thickness of cell walls and the degree of occlusion of the lumens of the cells. Some of this variation is correlated with ploidy particularly the size of the cells, thickness of cell walls and to some extent scale length, but these correlations are not constant over the whole of Africa. Scales representing the three principal levels of ploidy in South Africa are illustrated in fig.4. and show some of the differences between ploidies in this part of the continent. Within any level of ploidy it is difficult to detect any tangible differences useful over the whole continent, and difficulties in characterisation of the rather vague differences noted means that they have not been useful to any great extent.

iii) Ramenta.

The ramenta of small scales and fibrils present on the stipe, rachis and undersurface of the pinnae is partially deciduous, and rubs off very easily. Therefore, although in some cases there are considerable differences in quality and density, this feature cannot

be used very successfully on herbarium material.

iv) Frond shape.

Frond shape varies from lanceolate, sometimes with markedly decrescent pinnae, to deltoid. It has not been possible to detect any major discontinuities in this character though it has proved useful once at the tetraploid level in distinguishing one form (see p. 29).

v) Degree of Dissection of the Frond.

All fronds are at least bipinnatifid and may be cut very finely to a quadripinnatifid state. This character is especially significant with regard to the level of ploidy (see next section) but its potential usefulness is lessened by its plasticity, which is partially conditioned by age and luxuriance of any particular specimen. The character has been measured by counting the number of pinnules or lobes of the median pinna which are cut more than ⅔rds of their length to the costa. Alone the character shows a continuous grade of variation but in combination with spore size (see next section) it shows some correlation with the grade of ploidy.

vi) Spores.

The characters available from spores proved to be somewhat complex and they may therefore conveniently be dealt with in a separate section which follows.

SPORE SIZE.

In an attempt to offset the paucity of straightforward morphological characters, it seemed profitable to try to sort the herbarium material into grades of ploidy by means of spore size measurements. Some trial spore measurements on plants of known

chromosome number revealed differences in mean spore sizes. The histogram in fig. 5 shows the order of the differences in spore length between the three different levels of ploidy in South Africa, and such a difference in the means, if repeated elsewhere, might make it possible to sort the herbarium material into groups corresponding to probable ploidy, regardless of their morphology.

The results of this attempt are expressed on scatter diagrams in two ways, by combining spore length with either the degree of dissection of the frond or the length-breadth ratio of the spore. Fig. 6 records the incidence of spore size and degree of dissection in material from S. Africa, and fig. 7 records similar observations in material drawn from the whole of Africa. In both diagrams the material falls into three groups corresponding to the three grades of ploidy, the group with the smallest spores being sexual tetraploids, the one immediately above being sexual octoploids. The group with the largest spores consists of material of two breeding systems, one of which is sexual dodecaploid and the other apogamous.

The diagrams show a progressive reduction in the range of the degree of dissection of the sexual cytotypes with the rise in ploidy, the reduction being polarised on the lower end of the scale. Thus the tetraploids show the greatest and the dodecaploids the smallest range but the latter still covers the lower end of tetraploid range. Each of the three groups therefore show considerable overlap, which explains the continuous variation of this feature mentioned earlier. The reduction in the cutting of the fronds is often accompanied by a decrease in the size of the plants.

The apogamous plants are often more finely dissected than the sexual dodecaploids and their ploidy is less (mainly octoploid with a few decaploids). The large spore size associated with the apogamous habit (for further explanation see p.93) causes them to fall within the group of sizes characteristic of sexual dodecaploids. However they possess broader and more spherical spores than the sexual plants, and can usually be distinguished from the latter by this means.

The characteristic spore shape of the apogamous plants has been utilised, on scatter diagrams recording the incidence of spore length and length-breadth ratio, to differentiate them from sexual dodecaploids. These diagrams still separate the tetraploids and octoploids so that similar diagrams have been plotted for most of the herbarium material. It has been convenient to deal with these data regionally because of the number of specimens involved, and a diagram for cytologically examined representatives is illustrated in fig. 8 and those for herbarium material from different regions are shown in figs. 9 - 14.

The diagram (fig. 8) compiled from data obtained from plants of known chromosome number shows the positions the different sexual cytotypes and the apogamous forms may be expected to occupy. There is a good match between this diagram and those for the herbarium material from South Africa (fig. 9) and Southern Rhodesia, etc. (fig 10) indicating the presence of all three sexual cytotypes and the apogamous forms in these areas. In the latter diagram (fig. 10) however there is poor separation of the apogamous group from that denoted by open circles,, which is thought to be sexual dodecaploid. It has unfortunately not been possible to confirm cytologically that this last group is dodecaploid, but two

spore collections from it have on germination given rise to sexual prothalli. Although the apogamous and suspected dodecaploid groups in Southern Rhodesia coalesce on the diagram, it has been possible to separate them using frond morphology, spore ornamentation and by counting the number of spores per sporangium in very difficult cases; {apogamy being characterised by only 32 spores per sporangium}.

In East Africa much of the herbarium material falls into groups (fig 11, solid circles) corresponding in position to those seen for the sexual tetraploid and octoploid cytotypes and the apogamous forms in the previous diagrams. The situation in this area however is complicated by the presence of sexual tetraploids and octoploids, which show larger spores than are normally shown by these two levels of ploidy. They are represented on the diagram (fig. 11) by the open circles. The tetraploid is mainly from one high altitude locality (Aberdare Mtns., Kenya) and displays spore sizes intermediate between other tetraploids and the majority of the octoploids. The larger spored octoploid falls in a similar position to sexual dodecaploids on other diagrams, and will be dealt with as a separate taxon, A. demerkense Hier., since it can be separated from other E. African material morphologically as well as by its high altitude habitat. There are, however, other large spores on the diagram for Kenya and Uganda which could indicate a sexual dodecaploid in this region, but as yet no cytological evidence is available.

The diagram for W. Africa (fig. 12) shows groups corresponding to sexual tetraploid and octoploid cytotypes, but with rather poor separation. In addition one almost certain apogamous specimen is recorded, but there is no evidence from spore measurements carried out on existing herbarium

material to suggest the presence of a sexual dodecaploid on the mainland in W. Africa. The dodecaploid cytotype, however, is known from two of the offshore Atlantic Islands, Madeira and St. Helena, and is suspected of being present also on the Cape Verde Islands. On the diagram for the Atlantic Islands (fig.13) the herbarium material of these sexual 12ploids is separated most effectively from most of the material from the Canary Islands, which falls in a position typical of apogamous plants. Nevertheless two specimens from the Canaries show a spore length-breadth ratio more typical of sexual plants and as they fall on the diagram just below the sexual dodecaploids their ploidy is uncertain but they could be octoploid.

From the scatter diagrams it is evident that some success in dividing the herbarium material into groups corresponding to the different grades of ploidy known has been achieved, although the difference in spore size is not always so great as those shown by the living representatives. This is perhaps to be expected when dealing with considerable numbers of herbarium specimens of different ages, at different stages of spore maturity and sometimes yielding poor spore samples. These variables can be eliminated to some degree when measuring spores from plants in cultivation.

Methods of this sort can only be effective with fertile herbarium specimens and with close correlation of their spore size with that of cytologically examined representatives. For some parts of Africa certain features on these diagrams cannot be explained because of the lack of cytologically examined representatives. One example has already been provided by the large spores on the Kenya Uganda diagram (fig. 11).

A further example is afforded by the small amount of herbarium material from the Sudan and Ethiopia (apogamous excepted), which has shown spore sizes somewhat intermediate between typical sexual tetraploid and octoploid groups. As no cytological sampling has been possible the pattern of ploidy here cannot be established, and for this reason the material will be omitted from any detailed morphological treatment of the different cytotypes.

In spite of the defects mentioned and the possibility of undetected anomalies similar to the larger spored tetraploids and octoploids from East Africa, it is felt that the results provide a basis for determing the geographical distribution of the sexual cytotypes and the apogamous forms, as well as justifying a more detailed morphological presentation of each level of ploidy.

The morphology of the sexual forms within each level of ploidy and correlation of the variation with any species or varieties already described is the subject of the next chapter. The apogamous material except that from Southern Rhodesia can be effectively separated from the rest of the complex using spore measurements, and since it has not yet been possible to hybridise any of the apogamous plants with sexual forms they will be dealt with separately in Chapter VI.

Addendum: Some viable spores of the more spherical type have been generously provided by G. Kunkel from a herbarium specimen (no. 6722) collected by him on La Palma, Canary Islands. Since this chapter was written the prothalli raised from these spores have produced apogamous outgrowths thus confirming the prediction made on page 24 that apogamous plants are present in the Canary Islands. (see Table I, p. 95)

III. MORPHOLOGY, CYTOLOGY AND ECOLOGY WITHIN THE SEXUAL POLYPLOID GROUPS.

A. TETRAPLOIDS.

Two of the tetraploids within the complex have previously been described as A. furcatum Thunb. var tripinnatum Baker and A. milbraedii Hieronymus. The latter taxon is easily characterised and its merits will be discussed on p. 35. Baker's varietal epithet on the other hand could be applied to most of the more finely dissected and hence tripinnate forms of the complex. These are not easily defined though there are some regional differences. The same is true of the less deeply pinnate tetraploids (see scatter diagrams) which would not be treated as var tripinnatum Baker. For this reason, in the account which follows, the various main types with which I have been concerned will be dealt with in order under geographical headings.

A. aethiopicum (Burm.) Bech. var tripinnatum Baker.

A. furcatum Thunb. var tripinnatum Baker, Syn. Fil., 487, 1874.

The variety was first described by Baker in 1874 as "lower pinnae 2 in. br., bipinnate, with distant pinnules and obovate cuneate lower segments 1/8 - 1/4 in. br. Hab. Natal, Gerrard 592, Buchanan, McKen." It is clear that Baker was referring to the South African tetraploid material, which in its normal state is usually tripinnate, and the variety was recognised by Sim in both editions of "The Ferns of South Africa."

My own tetraploid tripinnate material may be treated as four more or less separate groups according to the geographical areas, S. Africa and S. Rhodesia, Vumba Mountains, Mt. Kilimanjaro and the Aberdare Mountains.

"var Tripinnatum". South Africa and Southern Rhodesia.

My own material from this region can be described as follows.

Description: Rhizome creeping and clothed in brown scales 5 - 9 mm. long. Scales clathrate and lumens of the cells not normally occluded. Fronds large, usually 2 - 3 feet (60 - 90 cm.) but sometimes up to 4 feet (120 cm.) long, deeply tripinnatifid to tripinnate. Stipe 10 - 50 cm. long, brown to dark brown and clothed, densely at the base, with small light brown scales and fibrils. Rachis also scaly and fibrillose, and on the upper grooved surface brown for one to two thirds of the length of the lamina then turning green. Lamina narrowly elliptic or lanceolate to elliptic or narrowly ovate, with 14 - 26 pairs of subopposite pinnae. Pinnae subcoriaceous and drooping, up to 13 cm. long and 6 cm. broad with a shining upper surface in live specimens, sparsely fibrillose on the underside, and cut into 7 - 15 often distant pinnules. The basal pair of pinnules on a pinna form an obtuse angle and in larger specimens are sometimes slightly reduced. Pinnules cut into 3 - 7 distinct segments, and the largest of these sometimes cut again into 3 lobes. Pinnules cuneate ovate becoming ovate as their size decreases and the pinnule segments obovate cuneate. All ultimate lobes with irregular furcate teeth. Spores with a conspicuous perispore wing.

(Silhouettes of three mature fronds are illustrated in figs. 14 - 16 and spores are shown in fig. 28a).

The following specimens have been cytologically examined:

B.38. Hogsback Forest, Amatola Mtns., Cape, S. Africa.

684-51. Amatola Mtns., Cape, S. Africa. (coll. Schelpe).

B.40. Engele Forest, Cape-Natal border, S. Africa.

B.157 Ceylon Ft. Reserve, Transvaal, South Africa.

B.190. Nr. Graskop, Transvaal, S. Africa.

B.211. The Pinnacle, Graskop, Transvaal, S. Africa.

B. 252. Woodbush Forest Reserve, Transvaal, S. Africa.

McNeil, s.n. Transvaal, S. Africa.

Mitchell 131. Inyanga, S. Rhodesia.

669 - 55. Penhalonga Waterfall, S. Rhodesia-Mozambique border, (Coll. Schelpe).

719 - 55. Gorongosa Mtn., Mozambique. (Coll. Schelpe).

Ecology and Distribution: Ecologically this tetraploid is confined almost exclusively to forest and in my personal experience in South Africa was always terrestrial, growing on the forest floor, rock (fig. 17), or old fallen tree trunks. Whenever encountered it was always locally abundant in the less densely shaded parts of the forest, at altitudes ranging from 2000 feet in the Eastern Cape to 5-6000 feet on the Drakensberg in Natal and the Transvaal. Occasionally it was found in more open habitats such as those caused by a rock fall in the forest or on rocky outcrops in or just above the forest, and in these latter situations it was often rather xeromorphic. At one locality in the Eastern Transvaal this tetraploid was the dominant fern growing in the open on the north side of a ravine at approximately 4000 feet. This population was very vigorous (fig. 18), and was probably able to occupy such a habitat through the frequent provision of moisture by mists and the partial shade afforded by the side of the ravine. It was noted in the field that plants in deeper shade generally did not produce sori so readily as those occupying more open and consequently less shaded situations in forest.

The tetraploid is again associated with forest in Southern Rhodesia

and Mozambique, occurring at altitudes of 4-7500 feet. Collectors' remarks indicate that it is nearly always a lithophyte on forest margins, etc, but it may sometimes be found as a low level epiphyte near the base of tree trunks or associated with rocks at the higher altitudes, often producing more xeromorphic forms.

The principal distribution is shown in fig. 25, and extends from the Eastern Cape to the Transvaal in S. Africa and along the Southern Rhodesia-Mozambique border. This distribution reflects that of the principal forested areas, which are mainly confined to the eastern mountainous rim or escarpment of the central plateau in southern Africa. It is interesting to note that the southernmost limit of the distribution in South Africa coincides with that of the summer rainfall area of the republic. Herbarium specimens closely resembling this tetraploid have been seen from Nyasaland, Northern Rhodesia and Uganda and the localities have been marked where possible on the map: however this material is rather scanty.

"var tripinnatum" Vumba Mtns., S. Rhodesia (and Mt. Mlanje, Nyasaland).

Material differing from the tetraploid just described in being more coriaceous and possessing markedly deltoid fronds and having pinnules with more entire segments which are less deeply toothed at their apices, was collected alive by Dr. E. A. Schelpe from the Vumba Mountains in Southern Rhodesia. This region also contains plants attributable to the previous tetraploid and others which tend to bridge the gap between the two extremes of frond shape.

A frond taken from the live plant in cultivation is shown in fig. 19. Although the chromosome number has not been confirmed the

spores from this frond fall within the size range of typical tetraploids, and the plant has been incorporated into the breeding programme as a tetraploid on this basis.

Herbarium specimens from the Mt. Mlanje area of Nyasaland are also more coriaceous and possess more deltoid fronds than the typical S. African tetraploids, but are never so markedly triangular as the Vumba specimen. They are also frequently larger than the latter with the pinnae bearing more distant and furcate pinnules. These Mt. Mlanje specimens differ from both tetraploids in possessing a darker tomentum on the base of the stipe as well as darker brown rhizome scales. They are either terrestrial or epiphytic, growing often in low forest at an altitude of 4500-6000 feet. No living representatives from this area have been available.

"var tripinnatum" Mt. Kilimanjaro, Tanganyika.

The most finely dissected tetraploid (fig. 20) so far known is found on Mt. Kilimanjaro; and can be described as follows.

Description: Rhizome creeping, with fronds semitufted at the growing point, and covered in small brown to dark brown scales. Scales 3-5 mm. long and $\frac{1}{2}$-$\frac{3}{4}$ mm. broad at the base. Fronds up to 4 feet (120 cm.) long and tripinnate to deeply quadripinnatifid. Stipe $\frac{1}{2}$-2 feet (15-60 cm.) long, light brown to brown and bearing a sparse tomentum of scales and fibrils in mature specimens, which usually thickens towards the base of the stipe. Lamina ovate to elliptic with 18-27 pairs of subopposite pinnae. Rachis fibrillose and brown on the upper surface for at least one third of the length of the lamina, the rest being green. Pinnae up

to 20 cm. long and 10 cm. wide with 17-29 pinnules. Pinnules up to 6 cm. long, overlapping markedly with those of the pinnae above or below, and cut into 4-7 obovate cuneate segments. The larger segments are deeply cut again into 3 or more narrow lobes which are in turn deeply incised at the apex into acute irregularly furcate teeth. The pinnules nearest the rachis of the larger pinnae are often slightly shorter than those in the mid-region of the pinnae. Spores are illustrated in fig. 28b and show a conspicuous perispore wing.

Unfortunately the live collections were lost because of delay during transit from East Africa, but the chromosome number of the following specimen has been inferred from a tetraploid hybrid synthesised (using wild spores) between it and a known tetraploid (see p.66)
B.366 G. Nr. Bismarck Hut, Mt. Kilimanjaro, 9300 feet.

Some herbarium specimens of this finely dissected tetraploid from this locality have previously been referred to as A. pergracile Rosenst. Although the type of this species has not been seen Rosenstock's description (1908) differs from the description above in some important respects. A. pergracile is described as possessing a long creeping rhizome with fronds, up to 50 cm. long, arising from it at intervals of 2-3 cm. This species is therefore much smaller than the tetraploid form of A. aethiopicum and possesses a longer creeping rhizome. In addition the lamina of A. pergracile is described as being bipinnate, and the nerves in the ultimate segments described as ending between the teeth and not in the teeth themselves. This last observation of Rosenstock's is clearly inaccurate, nevertheless, in view of the differences still

remaining it is felt that continuation of the practice of referring the tetraploid just described to A. pergracile Rosenst is unjustified.

Ecology and Distribution: (Fig 25.) This large and finely dissected tetraploid is known only from Mr. Kilimanjaro, where it was frequently encountered in the forest at 9-9500 feet, just behind the Bismarck Hut above Marangu. The forest here is very wet and mossy and in parts low and of an arborescent ericaceous type. The fern was terrestrial with the rhizome creeping through the thick moss carpet.

"var tripinnatum" Aberdare Mountains.

This group is rather heterogeneous morphologically but is suggested by the high altitude habitats and large spore size for the tetraploid level of ploidy (see p. 22), shown by a number of personal collections from the Aberdare Mountains. One form is described as follows.

Description: Rhizome creeping and clothed in dark brown scales 5 - 8 mm. long. Fronds up to 68 cms. long, deeply tripinnatifid to tripinnate. Stipe, sometimes longer than the lamina, dark brown to black usually becoming green towards the lamina on the upper grooved surface. Stipe and rachis both clothed thickly with dark brown scales and fibrils. Lamina 18 - 25 cm. long and 5 - 15 cm. broad, lanceolate or truncate narrowly-ovate to ovate. Pinnae deltoid, straight, stiff and coriaceous, with dark green upper shining surface. Undersurface fibrillose. Pinnae cut into 6 - 10 pinnules, the anterior and posterior pinnules nearest the rachis always being the largest. Pinnules cut into narrow obovate cuneate segments, which in the larger pinnules are again cut into 3 lobes. Ultimate lobes deeply incised

into narrow irregular teeth. Spores possess a conspicuous perispore wing.

(Silhouettes of two mature fronds are shown in figs. 21, 22, and a photograph of spores in fig. 28c).

The following two plants have been worked cytologically.
B. 451 Nyeri Chania Fall, Aberdare National Park, Kenya, 9500-10000 feet.
B. 462 Gimkururu Fall, Aberdare National Park, Kenya, c 10,000 feet.
The tetraploid level of ploidy has been inferred for the following plant from tetraploid hybrids (see p.63).
B. 448 B. Nyeri Chania Fall, Aberdare National Park, Kenya.

Ecology and Distribution: (Fig. 25). This tetraploid was collected at altitudes of 9 - 10,000 feet in the Aberdare Mountains on the plateau between Mt. Kinangop and Sattima. It was associated with low forest or shrubs around waterfalls in the river valleys, and was nearly always terrestrial except for the occasional very low level epiphyte.

Material differing from that described above in possessing larger often more deltoid fronds (up to 93 cm. long) with longer and narrower pinnae bearing more compact less dissected pinnules, was collected from two localities in the Aberdares. A frond is illustrated in fig. 23. It was growing in the open at both localities, one being beside a waterfall and the other on the roadside in bamboo forest, just below the tree line. An almost identical specimen has

been collected from a similar altitude on Mt. Kenya (Schelpe 2584 BM). This variant also resembles in some respects specimens from Mt. Mlanje, Nyasaland, already dealt with under the Vumba Mtns. group.

The following plant has been cytologically examined.

B.467. Queens Cave Waterfall, Aberdare National Park, Kenya, c.10,000 feet.

Further cytological observations: Two plants of this Aberdares group have shown a departure from the normal tetraploid number of 72 bivalents as follows.

B.467. 76 II's + 5 $\pm$ 1 I's. (fig. 24a,b.)

B. 451.72 II's + 2 I's.

This is the only region where irregularities in the chromosome number of this sort have come to my notice and it cannot be said with any certainty that similar departures are not present elsewhere. The detection of small abnormalities of this order requires preparations of unusual clarity and excellence, which are not easily obtained for every plant worked.

A. milbraedii Hier.

Type Descr: Deutsche Zentralafr. Exp. 2, 21, 1910.

A species which is being included in this section on tetraploids by virtue of spore size, no living material having been available for cytological examination.

A. milbraedii was described from material collected by Milbraed in the Lake Kivu region of the Belgian Congo and by Engler from the Usambara Mtns. in Northern Tanganyika. Hieronymus considered his new species as closely resembling A. furcatum Thunb. var tripinnatum Baker (then chiefly referring to S. African material) but distinguished it from this variety on the structure and form of the rhizome and rachis scales, their outer cells being made up of yellower walls and the inner of thicker darker brown walls, and also on pinnule shape, these being broader than those of the A. aethiopicum variety.

The type material from the L. Kivu region of A. milbraedii shows the rachis and pinnae to be sparsely adorned with small ovate acuminate scales differing from the more lanceolate rachis scales of A. aethiopicum var tripinnatum. On this character alone a number of specimens from the Kigezi District of Uganda and adjoining regions of the Belgian Congo may be attributed to this species. These also possess smaller more reddish brown rhizome scales ($2\frac{1}{2}$-5 mm. long), made up of thick walled cells with occluded lumens, and generally less dissected more compact pinnules than typical A. aethiopicum var trippinatum. In addition the spores have a slightly broader more transparent perispore wing. There are, however, two specimens from other parts of Uganda which

show rather intermediate characters and it is difficult to determine to which species they belong.

In spite of some difficulty in differentiating A. milbraedii from A. aethiopicum var tripinnatum it is felt that, until more material is available for morphological studies and live material can be incorporated into the breeding programme, the species can be usefully retained.

Less pinnate tetraploids

(excluded from var. tripinnatum).

The scatter diagram (fig. 7) showed some tetraploids with a low degree of dissection. These are never tripinnate, as far as can be ascertained, and for this reason cannot be included under var tripinnatum Baker. These forms fall into two main groups, one for East Africa and the other for W. Africa.

East Africa.

Description: Rhizome short creeping so that the fronds are markedly tufted at the growing point. Stipe black in dried specimens and clothed at the base in brown scales and fibrils becoming mainly fibrillose above. Fronds, bipinnate to tripinnatifid, up to 90 cm. long. Rachis fibrillose and green on the upper surface for almost the whole length of the lamina. Lamina lanceolate to truncate narrowly ovate or narrowly deltoid, with 10-17 pairs of subopposite pinnae, the lowermost pair being only slightly reduced if at all. Pinnae, generously spaced and never markedly overlapping, smooth, thin but coriaceous, shining on the upper surface and sparsely fibrillose on the undersurface. Pinnae cut into 3 - 9 pinnules only 1 - 4 of these being petiolate. Pinnules narrow obovate cuneate to ovate cuneate in the largest. Largest pinnules further cut into 3 - 5 lobes but never markedly tripinnate. Spores with a shallow and inconspicuous perispore wing.

(Silhouettes of fronds from two plants are illustrated in figs. 26, 27, and spores are shown in fig. 28 c).

The following representatives have been examined cytologically.

B.418.A. Mt. Kilimanjaro, Tanganyika, c. 6000 feet.

B.418.B. Mt. Kilimanjaro, Tanganyika, c. 6000 feet.

B.487. Kericho, Kenya, 6000 feet.

342/55. Kenya. (Panigrahi plant).

B.478. Tusha Ft. Reserve, Aberdare Mtns., Kenya, c. 7000 feet.

This group as exemplified by B. 418 and B. 487 shows a tendency to become tripinnatifid in the latter, but these specimens are nevertheless rather distinct from the tetraploids dealt with under var tripinnatum because of their narrower pinnules and smoother appearance of the fronds. Plants from slightly higher altitudes of 7-8000 feet on Mt. Kilimanjaro tend to be more fibrillose than B.418 and with broader and more deeply lobed pinnules so that the fronds are sometimes nearly tripinnate. Similar morphological tendencies are shown by the collections from the Tusha Ft. Reserve on the Aberdare Mountains and one specimen collected from this locality is very close to the Aberdare tetraploid group in its degree of dissection, but does not display the same large spores.

Ecology and Distribution: This tetraploid occurs in forest in East Africa at altitudes ranging from 4200 feet to approximately 8500 feet. On Mt. Kilimanjaro material was collected from 6000 to about 8500 feet and it was always epiphytic from a few to 20 or more feet from the forest floor. The Tusha Forest Reserve collections were also epiphytic, but the two plants seen at Kericho were terrestrial at the forest edge on a river bank. Although always associated with forest it shows a

preference usually for less densely shaded parts.

Herbarium specimens suggest this tetraploid is widely distributed in East Africa particularly in Kenya, collections having been seen from Mr. Kenya, Aberdare Mountains and Mau Forest and Escarpment regions. It probably extends eastwards to Mbale in Uganda. Specimens, it appears, had not previously been collected from Mt. Kilimanjaro. The southernmost limit of this tetraploid is uncertain since herbarium material of the complex generally is scanty from Tanganyika. There are, however, some less dissected specimens from Nyasaland and Northern Rhodesia, but these are generally more fibrillose and possess broader pinnules than the typical specimens from Kenya. The distribution is shown in fig. 30.

West Africa.

The scatter diagram for spore sizes of herbarium material from West Africa (fig. 12) shows poor separation of possible tetraploids and octoploids. However the uncertainty regarding probably ploidy applies only to a few specimens and a number of them are thought to be almost certainly tetraploid. Many of these show a degree of dissection and spore ornamentation similar to the East African tetraploid but the fronds do not possess the same smooth appearance, being often densely scaly and fibrillose with the lower pairs of pinnae sometimes markedly decrescent. Further specimens from S. Tomé and one from Angola have even less dissected fronds being commonly bipinnatifid.

Only one living representative from West Africa has been available which is not typical morphologically, but as it has been used in the breeding programme its principal features will be described.

Description: Short creeping rhizome appearing almost as if erect, so that the fronds tufted. Stipe short and densely fibrillose as are the rachis and undersurface of the pinnae. Fronds up to 55 cm. long, linear-lanceolate, bipinnate although sometimes only deeply bipinnatifid, with 15 - 30 pairs of pinnae. The pinnae in the lower half of the frond slightly decrescent and reflexed. Pinnae up to 5 cm. long and $1\frac{1}{2}$ - 2 cm. broad, cut into 5 - 9 lobes, the anterior in larger specimens being cut down to midrib forming a distinct pinnule. Pinnules slightly cut again into 3 lobes. Pinnae lobes tapering gradually into a long point and curving slightly inwards towards the mid line of the pinnae. All ultimate lobes truncate and serrate at the apex. Spores possess a shallow and inconspicuous perispore wing.

A frond from the living representative is illustrated in fig. 29 and the locality is given below.

K. 100. Cameroons Mtn., Lake Barombela, c. 5000 feet, epiphytic.

Distribution: The distribution of the West African tetraploid group is shown in fig. 30.

The map shows that the suspected tetraploids on the mainland are confined to the principal mountainous area around the Cameroons. Although ecological information is scanty the plants would appear to be always associated with forest (as for tetraploids in other parts of the continent) and can be either epiphytic or terrestrial.

The few specimens from S. Tomé and Angola are also represented on the map but tetraploids have not been confirmed cytologically from either of these two localities.

B. OCTOPLOID.

With one notable exception (A. demerkense Hier.) the octoploid members of the complex are even closer to each other morphologically than the tetraploid forms and the detection of variation on a regional basis has been almost impossible. Nevertheless certain morphological tendencies between some localities have been noted but since these are only tendencies it is proposed to deal with the octoploids as one group, apart from the exception mentioned, under the name of A. aethiopicum (Burm) Bech.

A. aethiopicum (Burm) Bech. sens. strict. Candollea VI, 23, 1935

Trichomanes aethiopicum, Burm. Fl. Cap. Prodr. 28, 1768.

A. falsum, Retz. Obs. vi, 38.

A. furcatum, Thunb. Prod. Pl. Cap. II: 172, 1800

The material on which Burmann based his original description of Trichomanes aethiopicum came from the Cape and was described as "Frondibus bipinnatis, pinnis alternis, pinnulis pinnatifido - incisis glabris." Specimens from the same region were later described as "pinnulis obovatis, incisis serratis, stipite hirto" under A. furcatum by Thunberg. Spores measured from the holotype of A. furcatum agree in size with those of known octoploid material from the Cape, indicating that this type specimen is almost certainly octoploid material. This is further substantiated by the cytological findings presented in this thesis that only the octoploid level of ploidy is present in the Cape region. Burmann's original specimen has not been available but in view of the cytological uniformity so far evident for the complex in

the Cape region it seems likely that this type is also octoploid material. Therefore the name A. Aethiopicum in its strictest sense should probably be applied to the octoploid cytotypes only, though to do this might prove impossible (for further discussion see p. 48).

The following description of the octoploids has been drawn up from my own personal material which shows a similar range of variation to the suspected octoploids in the herbaria.

Description: Rhizome stout, short creeping, and clothed in reddish-brown to nearly black scales 5 - 10 mm. long. Scales clathrate with little differentiation of constituent cells and usually with a long hair point. Lumens of cells may be open or occluded, the latter particularly in the vertical median line and near the apex of the scale. Fronds 15 cm. to 90 cm. but most frequently 30 - 60 cm. long, with a tomentum of dark brown scales and fibrils on the stipe, rachis and undersurface of the pinnae. Fronds bipinnatifid to deeply tripinnatifid but never markedly tripinnate. Lamina lanceolate, narrowly ovate to ovate and sometimes nearly deltoid. Pinnae subopposite and often stiff, the lowermost pair of the lamina or one or two pairs above commonly the longest but sometimes the pinnae are markedly decrescent in the lower part of the lamina. Pinnae coriaceous, upper surface dull with few fibrils, 2 - 15 cm. long and $1\frac{1}{2}$ - 9 cm. broad with 1 - 11 distinct pinnules and a number of lobes tapering to a point. The largest anterior and posterior pinnules are often neither markedly obtuse or acute. Pinnules subflabellate, divided into 3 or in larger specimens up to 6 or 7 further segments. Ultimate segments or lobes

irregularly serrate at the margin or more deeply incised into irregular furcate teeth. Spores variable with the perispore wing well developed in many plants but grading into specimens possessing spores where the perispore wing is shallow and relatively inconspicuous.

(Silhouettes of fronds from octoploid plants collected from different parts of Africa are assembled in figs. 31 - 39 and four samples of spores are illustrated in fig. 40.)

The following material has been cytologically examined.

South Africa.

B. 1. Pipe Track, Blinkwater, Cape Peninsula.

B. 2. " " " " "

B. 3. " " " " "

B. 6. Skeleton Gorge, Kirstenbosch, Cape Peninsula.

B. 263. Window Gorge, Kirstenbosch, Cape Peninsula.

Schelpe 4281. Between Knysna and Gouna, Knysna Div., Cape.

B. 17. Gouna, Knysna Forest, Cape.

B. 20. Between Knysna and Gouna, Cape.

B. 24. Platbos Ft. Reserve, Humansdorp Div., Cape.

B. 112. 1 mile N. of Dohne, Stutterheim Div., Cape.

B. 115. Kologha Forest, Stutterheim Div. Cape.

B. 214. The Pinnacle, Nr. Graskop, Pilgrims Rest Div. Transvaal.

Southern Rhodesia.

Williams U.H.T. 10. Murakwa's Hill, Umtali, S. Rhodesia.

East Africa.

B. 313. Lushoto, Usambara Mtns., N. Tanganyika.

B. 400. Marangu, Mt. Kilimanjaro, c. 4500 feet.

342/55. Kenya.

B. 437. By Chania River, Nyeri, Kenya.

B. 484. Kericho, Kenya.

B. 485. Kericho, Kenya.

Tweedie 1815. Mt. Kenya.

West Africa.

Hambler 211. Nigeria, Mt. Cameroons, Stream Valley, above Hut II.

280/57. Cameroons Mtn.

Distribution: The distribution compiled from herbarium records and fieldwork is shown in fig. 41. The octoploid cytotype covers a geographical area similar to that of the tetraploids with two marked extensions beyond the known distribution of the lower ploidy. One of these extensions occurs in South Africa and the other in West Africa. In South Africa they extend south-westwards from the summer rainfall area into the Mediterranean Cape region, which stretches from Knysna to the Peninsula. In West Africa the octoploid distribution may well extend to the Canary Islands whilst the tetraploid is confined to the Cameroons area. In view of the uncertainties regarding the ploidy of the material from the Sudan and Ethiopia (see p. 25) this is not plotted on the map, but it may be noted that if much of this material is octoploid as seems likely, then a further departure of the octoploid from the tetraploid distribution would be indicated.

Ecology: The South-Western Cape of South Africa with a mediterranean climatic régime receives the bulk of its rainfall during winter (June to September): the summer being long and dry. In this region octoploid A. aethiopicum was frequently encountered on the Cape Peninsula and mountains further east.

On the Cape Peninsula the octoploid was always found growing terrestrially (fig. 42) at altitudes from near sea level to 3000 feet. It was generally associated with the wooded slopes, kloofs and ravines on both sides of Table Mountain and the Peninsula further south. It was also seen in more open situations among boulders, in rock crevices or on open rock, particularly in the mist zone of the mountain, and if in such habitats at lower altitudes the plants were usually shaded by small trees or shrubs. In the drier of these more open habitats plants were very often small and xeromorphic.

Similar field observations were made for the octoploid on the Cape mountains further east in the winter rainfall area (fig. 43).

The main growth period of this cytotype in the South-West Cape coincides with the winter rainfall season, but growth is usually most marked in late autumn and spring and almost ceases during the long dry summer. Plants in more exposed habitats may dry out completely in summer, appearing as if dead. However the rhizomes of specimens examined in this condition were still fresh and would doubtless put up new fronds on being moistened again in autumn.

Further east in the Knysna area, where rain falls all the year round, the octoploid was only seen in forest and although locally frequent it was never abundant. The plants were mainly terrestrial

but a few were seen growing as epiphytes on dead Cyathea trunks. They were never seen in the darker and wetter parts of the forest.

The octoploid is again confined mainly to forest in the summer rainfall area of Cape Province, further east from Knysna. Here it was seen as a low level epiphyte (fig. 44) with tetraploids sometimes growing in the same locality as in the Kologha Forest near Stutterheim. This pattern was again observed in Natal and the Transvaal but the octoploid was frequently epiphytic at greater distances from the forest floor. At Woodbush in the northern Transvaal specimens were never seen less than 15 feet from the forest floor and were often much higher, which made collection difficult.

The octoploid cytotype in South Africa , then is primarily associated with forest although in the South West Cape particularly it can also occupy more open, drier situations than are found in typical forest. There is also, from the Cape north-eastwards to the Transvaal, an increasing tendency for the octoploid to assume an epiphytic habit. The herbarium material confirms this observation but there are, nevertheless, some terrestrial specimens from Natal and the Transvaal. It is interesting to note that whereas in the Cape and Knysna areas the octoploid is fairly frequent and the tetraploid is absent, in Natal and the Transvaal it is relatively infrequent while the tetraploid is often abundant.

In Southern Rhodesia the octoploid as far as can be ascertained from herbarium specimens shows a preference for the epiphytic habit in forest but this is by no means exclusive. In East and West Africa no pattern emerges regarding growth habit, epiphytic specimens being as

frequent as terrestrial plants. Nevertheless in these areas the octoploids appear to be primarily forest ferns, often growing in the same locality as tetraploids.

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The octoploid material illustrated in figs. 31 - 39 shows some of the variation in frond morphology within the cytotype. However as stated earlier at the beginning of the section this variation does not lend itself to treatment on a regional basis in the same way as that of the tetraploids. Nevertheless it is interesting to note that the specimen from West Africa illustrated in fig. 39 shows descrescent pinnae in the lower half of the frond: a feature already seen in the tetraploid from this area (fig. 29).

The variable nature of the spores of octoploids has already been noted in the description and there is some correlation between their ornamentation and the terrestrial and epiphytic modes of growth recorded for the octoploids in the ecological section. Those plants possessing spores with an inconspicuous shallow perispore wing are generally epiphytic while spores with broader more cristate perispore wings tend to be associated with often larger terrestrial plants. Two examples quoted from personal field experience will serve to illustrate this point further. In South Africa the octoploids from the Cape Peninsula to Knysna (nearly always terrestrial) generally possess spores of the type shown in fig. 40a, while the spores in fig. 40b are from an epipbytic octoploid collected in the Transvaal. Two octoploids from the same locality at Kericho, Kenya, again show the two types of spore ornamentation. The spores of the larger terrestrial octoploid B. 485 are illustrated in fig. 40c and those of the smaller epiphytic plants B 484 in fig. 40d. The correlation

between spore ornamentation and growth form is not absolutely consistent and although in the illustrations the two types of spore ornamentation are distinct they do tend to intergrade.

It was seen from the scatter diagrams that some success could be achieved in dividing the tetraploid and octoploid material by measuring spores. It was then possible to investigate if a similar separation could be effected by more conventional morphological methods.

It is possible to separate the tetraploids dealt with under A. aethiopicum var tripinnatum from the octoploids fairly satisfactorily using frond characters, particularly in southern Africa. However in areas where less pinnate tetraploids are present the problem is much more difficult since these resemble the octoploids much more closely in the degree of dissection of their fronds than do the tripinnate forms. In these areas, e.g. Nyasaland, East Africa and West Africa, separation of the two ploidies is not always possible without resorting to spore measurements, even to one familiar with the group. Furthermore separation by spore measurements is complicated by the presence of tetraploids with larger spores than are normally shown by this level of ploidy, which may approach or equal the size of octoploid spores. This has been seen to occur in East Africa (see fig. 11). Where no complication of this nature is evident separation may still be poor using spore measurements as in West Africa. It is therefore doubtful if a practicable separation of tetraploids and octoploids useful to both herbarium taxonomists and fieldworkers could be effected for the whole continent.

A. demerkense Hier.

Engler Jahrb. 46, 375, 1911.

The specimens from East Africa possessing a larger spore size than is normal for the octoploid level of ploidy and growing at high altitudes (see p. 23) resemble most closely A. demerkense Hier.

The cytologically examined material from Mt. Kilimanjaro may be described as follows.

Description: Stout creeping rhizome clothed thickly in dark brown scales up to 8 mm. long. Scales clathrate and made up of large cells with thick walls. Fronds 10 - 23 cm. long (occasionally up to 30 cm. long), bipinnatifid to bipinnate, and clothed usually very densely with reddish brown to brown scales and fibrils on all parts of younger fronds, but more particularly on the stipe, rachis and undersurface of the pinnae of older fronds. Stipes variable in length, the longer examples being up to 19 cm. long being one and a half to nearly twice the length of the lamina, while others are much shorter and only half the length of the lamina or less. Lamina 7 - 17 cm. long and 2 - 5 cm. broad, lanceolate to narrowly ovate in outline with 7 - 15 subopposite pairs of pinnae. The two lowest pairs of pinnae may be slightly reduced but generally the pinnae in the lower half of the lamina are of a constant width. Pinnae small, rhomboid or trapezo-rhomboid and acute, the largest cut into 1 or 2 distinct but rarely petiolate pinnules and 4 - 7 lobes tapering to a point. Pinnules slightly cut again into 3 lobes and the apices of all ultimate lobes with irregular furcate teeth. Sori when mature nearly always coalesce to form a dark brown mass of ripe sporangia.

(A silhouette of a plant is illustrated in fig. 45 and a frond from a further plant in fig. 46. Spores are shown in fig. 47.)

The localities of two cytologically examined plants are given below and a meiotic preparation from one of them showing n = 144 is illustrated in fig. 48.

B. 379. Mt. Kilimanjaro, Tanganyika, c. 11,000 feet.

B. 387. Mt. Kilimanjaro, just below Peters Hut, c. 12,000 feet.

The material described differs from the type specimen of A. demerkense in some respects. This specimen from Ethiopia is slightly larger showing glandular hairs on the margin of the indusium and does not possess a dense ramentum of scales and fibrils on the frond, although repeated handling may have removed the latter. The specimen does however match the material described above in the large cells of the rhizome scales, frond shape, pinna pattern, spore size, although the ornamentation differs slightly and it was collected from a similar altitude. The spore size was one of the features which drew attention to the similarity of the type of A. demerkense and the material described above; however its ultimate importance in this respect cannot be assessed until live material is available from the type locality for cytological study.

Previously some herbarium specimens similar to the material described have been attributed to A. demerkense while others have been placed under A. aethiopicum. All my own material and herbarium specimens examined are however reasonably distinct from A. aethiopicum. Therefore it is felt to be most satisfactory to place these specimens

provisionally under A. demerkense since the epithet is available. This treatment then recognises their morphological and ecological discontinuity from A. aethiopicum and at the same time does not conflict with partially established practice nor does it introduce a new specific epithet which would be unnecessary if their differences from the type specimen noted above proved unimportant taxonomically.

Ecology: On Mt. Kilimanjaro specimens were collected from 10,000 to 13,000 feet in the ericaceous shrub and Helicrysum zones. At these altitudes the mountain becomes progressively drier as altitude increases and has a marked diurnal variation in temperature typical of afro-alpine regions. The night temperatures fall to below freezing on many or most nights of the year whereas the day temperatures may be fairly high. A.demerkense was always associated with rocky outcrops, particularly in the valleys of small streams or on the edge of lava flows, growing in crevices or sometimes on rock exposed to full sun.

Similar specimens seen in herbaria have been collected from rock usually above the tree line at altitudes of 8600 - 13400 feet on other mountains. These include:- Marra Mtns., Sudan; Mt. Kenya; Mt. Hanang, N. Tanganyika; Mt. Elgon and Virunga Mtns., Uganda; Cameroons Mtn., W. Africa.

Distinguishing characters: The type specimen of A. demerkense possesses a stipe longer than the lamina part of the frond and Hieronymus quoted this feature as one of the characters distinguishing his species from A. aethiopicum (A.praemorsum Sw.). The variable

length of the stipe in relation to the lamina has already been noted in the description of my own material and field observations indicate that much of this variation is probably correlated with the particular habitat of the specimens. Plants growing in deeper more shaded crevices tend to produce larger stipes (fig. 46) while those on more open rock display shorter stipes (fig. 45), which makes the latter specimens smaller although the lamina part of the front is not substantially reduced.

The material dealt with here may however be distinguished from A. aethiopicum by the following characteristics:-

1) Small size of plants, fronds rarely being more than 23 cm. long.
2) Dense ramentum of scales and hairs on the stipe, rachis and undersurface of the pinnae.
3) Small but relatively finely dissected pinnae.
4) High altitude habitat.

C. DODECAPLOID.

The dodecaploid cytotype has been discovered in the complex to be associated with three different geographical regions, southern Africa, St. Helena and Madeira. The material from each of these areas is characteristic and it will therefore be convenient to deal with it under geographical headings as in the section on the tetraploids.

Southern Africa.

Description: A small fern with fronds rarely exceeding 23 cm. in length. Rhizome short creeping and covered in dark brown scales 3 - 6 mm. long (fig. 4). Fronds bipinnate, clothed in a persistent tomentum of small dark brown scales and fibrils particularly on the base of the stipe, rachis and undersurface of the pinnae. Lamina narrowly ovate to ovate in outline but often broadest at the lowermost pinnae or the pair above so that the frond often narrowly deltoid. Pinnae, 6 - 9 subopposite pairs and occasionally up to 11, coriaceous and blunt with the larger divided into 2 - 3 pinnules. Pinnules, spreading so that the two largest form an obtuse angle, lobed sometimes deeply into truncate segments. Spores possess a broad conspicuous perispore wing.

(A silhouette of a frond is shown in fig. 49 and spores in fig. 52.)

Two plants have been cytologically examined and their localities are given below:-

B. 128. New Chum Falls, Nr. Pilgrims Rest, Transvaal.

Nat. Herb. Pretoria. Wonderboom Reserve, Pretoria, Transvaal.

The group suspected of being dodecaploid on the scatter diagram for Northern and Southern Rhodesia (see fig. 10, also p. 22), is a good match morphologically to the South African dodecaploid material in most respects. The fronds, however, may be slightly longer and more dissected, sometimes reaching a deeply tripinnatifid condition. As mentioned on p. 22 young sporelings from two different localities in Southern Rhodesia are now available but are too young for cytological examination. Nevertheless in spite of the absence of any confirmation of the chromosome number of the Southern Rhodesian material it is being included here with the South African dodecaploid on morphological evidence alone.

Ecology: This dodecaploid group shows a striking departure from the forest habitats typical of the tetraploid and most octoploid forms within the complex. In South Africa these dodecaploids are essentially rock or rock crevice ferns; a habitat characteristic of many European spleenworts. B. 128 was collected on the high veldt in the Transvaal on a rocky outcrop bordering a river. Here it was found in shallow rock crevices exposed for part of the day to full sun. The population consisted of a few clumps made up of 2 or 3 plants each and was evidently very local since a further search in the neighbourhood yielded nothing. The other living representative listed above was collected from a rock crevice near a spring.

Information where available from herbarium sheets shows similar habitats; comments such as "Occasional in shaded rock crevices" (Repton 1037, PRE) and "Rocky hill slopes in crevices and under rock ledges" (Liversidge s.n., BOL) being typical. The altitude range in South Africa is 4800 to 6000 feet.

This group in Northern and Southern Rhodesia again shows a preference for habitats away from the main forested areas. Information recorded on herbarium sheets shows the plants to be associated with rock, usually granite, and rock crevices.

Distribution: The distribution data are plotted on the map in fig. 53.

The distribution pattern contrasts strongly with that shown by the two lower ploidies already discussed in that the dodecaploids show a spread towards the interior from the eastern edge of the central plateau in southern Africa. This is particularly evident in northern and southern Rhodesia and the Transvaal of South Africa, where the tetraploids and octoploids are confined mainly to forest on the eastern edge of the plateau. Since the rainfall falls off from the edge of the plateau towards the interior the dodecaploids in general occupy areas, which,for part of the year at least, are drier than those preferred by the two lower cytotypes.

The distribution extends southwards into Natal and the eastern Cape Province and the southernmost limit coincides with that of the tetraploids in South Africa (see fig. 25 and also p. 29) thus the dodecaploids are also confined to the summer rainfall area of S. Africa. In both these last two areas the dodecaploids occur below the escarpment forming the edge of the central plateau and are found again in generally drier regions than either the tetraploid or octoploid cytotypes.

St. Helena.

All herbarium specimens examined from St. Helena are extremely uniform morphologically and it seems likely that the only representatives

of the complex on the island are dodecaploid.

Description: Rhizome short creeping. Fronds deeply tripinnatifid up to 50 cm. long, smooth on the upper and lower surface, any scales and fibrils being confined mainly to the stipe and rachis. Lamina lanceolate to narrowly ovate nearly deltoid with 10-14 subopposite pairs of pinnae, the lowermost pair commonly being the largest. Pinnae smooth and fleshy, the largest being cut into 5 - 7 pinnules. Pinnules spreading, the basal anterior and posterior always forming an obtuse angle, deeply cleft into three spreading segments and these latter often cut less deeply into small truncate lobes. Spores with a shallow and inconspicuous perispore wing.

(A silhouette is shown in fig. 50 and spores in fig. 52).

The only plant which has been cytologically examined is one raised from spores taken from an herbarium specimen in the British Museum, the details of which follow:-

Kerr 137. Nr. Green Hill, St. Helena, In rock valley by stream, 1200 feet.

The St. Helena dodecaploid differs from that in southern Africa by a number of features other than its geographical distribution. These include:-

1) Larger fronds with a less dense ramentum and altogether smoother and fleshier appearance.
2) More finely dissected pinnae.
3) Spreading fan-like pinnules with linguiform lobes.
4) Spores with a greater length/breadth ratio, i.e. narrower.
5) Spores possess a very shallow and less conspicuous perispore wing.

Although differing from the dodecaploid group from southern Africa in these respects, the St. Helena 12ploid is nevertheless morphologically more closely allied to it than to the dodecaploid from Madeira, which will now be dealt with in the following subsection.

Madeira.

The first plant to show the 12ploid chromosome number within the complex came from Madeira. The herbarium material from the island is reasonably constant morphologically and a study of spore size indicates that the 12ploid is the only cytotype present.

Description: Rhizome short creeping, covered in brown scales which are occasionally fimbriate. Fronds bipinnatifid to bipinnate up to 45 cm. long and clothed densely in brown scales and fibrils on the stipe and rachis but less so on the underside of the pinnae. Lamina lanceolate with 10 - 18 pairs of subopposit pinnae, the lower 3 - 6 pairs being slightly decrescent or of a constant width. Pinnae narrow and tapering gradually to a point, lobed or in larger specimens cut into 1 or 2 distinct pinnules. The anterior and posterior lobes or pinnules of each pinna form an acute angle. Pinnules and lobes usually entire with irregularly toothed apical margins. Spores possess a well developed perispore wing.

(A silhouette of a frond is illustrated in fig. 51 and spores are shown in fig. 52).

Two living representatives have been available and examined cytologically.

Manton s.n. Santa de Serra, Madeira.

Manton s.n. Ribo Frio, Madeira.

Specimens in the herbaria of the dodecaploid material from Madeira have sometimes been referred to A. maderense Penny. It has however not yet been possible to typify this species satisfactorily since the description in Loudon's Hortus Britannicus consists only of horticultural details and no type specimen is known. It has therefore been preferred for the time being not to segregate this material under A. maderense Penny.

Some herbarium material collected from the Cape Verde Islands closely resembles the plants from Madeira and also show a similar spore size (see fig. 13). They may therefore be included in this group although no living material for confirmation of the chromosome number has been available.

Ecology: Typical habitats in Madeira for this dodecaploid are stone walls and fissures or crevices associated with them. No information for the Cape Verde Islands is available.

The dodecaploid from Madeira differs from those in southern Africa and St. Helena as follows.

1) Fronds lanceolate with the lower pairs of pinnae frequently being decrescent.
2) Fronds less dissected often being only bipinnatifid.
3) Pinnae narrow and acute tapering more gradually to a point.

IV. ARTIFICIAL HYBRIDS.

The plants used in the breeding programme are listed below and silhouettes of all of them may be found under the relevant morphological section. Reference is made to these silhouettes in brackets after each plant.

a) Tetraploids.

McNeil, s.n.	Transvaal, S. Africa.	(fig. 14)
Schelpe 5428 .	Vumba Mtns., S. Rhodesia.	(fig. 19)
B. 366 G.	Mt. Kilimanjaro, Tanganyika.	(fig. 20)
B. 448 B.	Aberdare Mtns., Kenya.	(fig. 22)
B. 418.	Mt. Kilimanjaro, Tanganyika.	(fig. 26)
K. 100.	Cameroons Mtn., W. Africa.	(fig. 29)

b) Octoploids.

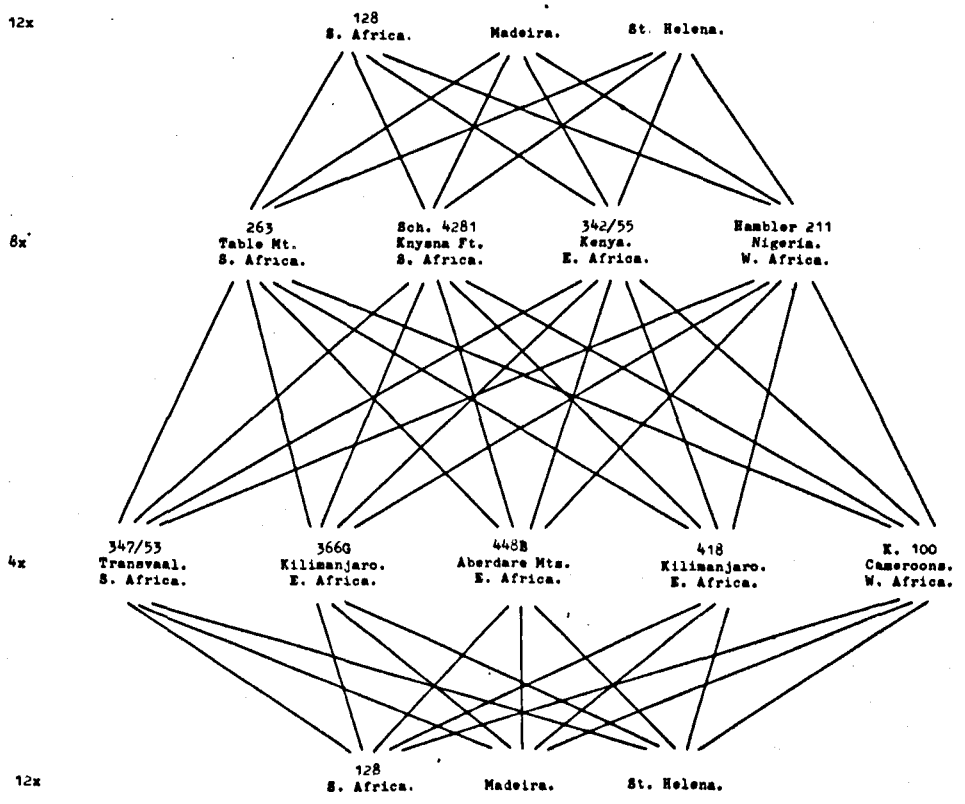
B. 263.	Cape Peninsula, S. Africa.	(fig. 32)
Schelpe 4281.	Knysna Ft., Cape, S. Africa.	(fig. 34)
342/55.	Kenya.	(fig. 38)
B. 484.	Kericho, Kenya.	(fig. 36)
Hambler 211.	Cameroons Mtn., West Africa.	(fig. 39)
B. 379.	Mt. Kilimanjaro. (A. demerkense)	(fig. 45)

c) Dodecaploids.

B. 128.	Transvaal, S. Africa.	(fig. 49)
Manton, s.n.	Madeira.	(fig. 51)
Kerr. 137.	St. Helena.	(fig. 50)

The hybridisation diagram on the following page shows the crosses which have been made between plants of different ploidies.

The diagram, however, does not show the hybrids which have been synthesised between plants with the same chromosome number: thus the plants in each horizontal row on the diagram have been crossed in all possible combinations.



HYBRIDISATION - A. AETHIOPICUM.

In addition the octoploid A. demerkense Hier. has been combined with all the octoploids and dodecaploids and the tetraploids B418, B366G, B448B and K100. The probable tetraploid Schelpe 5428 and the octoploid B484 were introduced into the hybridisation programme at a late stage and have been crossed with a number of other tetraploids, octoploids and dodecaploids:

Clearly with such a formidable array of hybrids and also as many are not yet old enough for meiotic studies, it has not been possible to obtain the information required from all of them. Only those hybrids which have yielded information on either chromosome pairing at meiosis or fertility will be mentioned further. These will be arranged in groups under the heading of the chromosome number which would be expected from that of their parents.

Hybrids on the whole were easily synthesised and no conspicuous barriers appear to exist which prevents the crossing of any of the various cytotypes or forms within each cytotype. For this reason details of the number of hybridisation attempts and percentage success for each cross will be omitted. In the treatment which follows each cross will be given roman numerals for ease of reference and individual plants will be identified by the number of hybridisation attempt, which will be followed by the analyses obtained from meiotic preparations and information on fertility. Each group of hybrids will be concluded by a summary of chromosome analyses and their interpretation in preparation for fuller discussion in Chapter VII.

The difficulties encountered in obtaining cytological information from the hybrids have already been referred to in the Materials and Methods (see p.12) together with the fact that it has not generally been possible to determine the numbers of multivalents accurately. Complete accuracy therefore cannot be claimed for any of the analyses from hybrids above the tetraploid level of ploidy but the margin of error is not so great as to invalidate the conclusions to be drawn from them in this thesis. For the analyses of cells where multivalents

formation is noticeable the word 'associations' will be used to denote bivalents and possible multivalents. Some indication of the number of multivalents may then be obtained from the difference between the chromosome total obtained where all the associations are considered as bivalent and the total expected from the ploidy of the parents. Thus for a hexaploid hybrid (n = 108), an analysis of 72 associations + 56 univalents would allow for the presence of 16 trivalents.

TETRAPLOID HYBRIDS.

There are seven hybrids of this composition, which have become mature enough to work cytologically, involving 5 different tetraploids combined as shown in the diagram fig. 54. A diagrammatic summary of the cytological results will be found on p. 66.

(i) B 418. 4x Kilimanjaro X B. 448.B. 4x Aberdares.

This cross is being dealt with first as it illustrates both the difficulties associated with the pairing of the chromosomes in some of the hybrids and the unreduced gametes which have been encountered in the hybridisation programme.

The following analyses have been obtained from one hybrid at three different times.

AB. 323. A.	23/5/63.		144 I.	(5 cells)
	4/11/63.	42 - 61 II +	22 - 60 I.	(3 cells)
	17/3/64.	69 II +	6 I.	

It is not certain that the increase of the chromosome pairing with ageing of the plant shown by these figures is a simple relationship, since between the two last dates the hybrid was repotted and moved to a cooler greenhouse. Nevertheless they do show clearly the necessity during this investigation to re-examine plants showing a low order or complete failure of chromosome pairing at meiosis.

Results from other hybrids of the same cross:

AB. 322.A.	70	II	+	4	I.	
AB. 403.A.	71	II	+	2	I.	(2 cells)
	69	II	+	6	I.	
AB. 403.B.	72	II				(3 cells) (fig. 55)
	71	II	+	2	I.	

These plants all produce a high proportion of good spores but a small amount of abortion is present. Samples sown from plants AB. 322.A. and AB. 403.A. have germinated and the prothalli are now producing young sporophytes.

(ia) One plant from this cross is hexaploid and approximate analyses of two cells are given below.

AB. 322.B.	75 associations	+	60	I.	
	77 "	+	56	I.	

The spores are abortive but the plant is otherwise similar to the tetraploids above and must have arisen as a result of the functioning of an unreduced gamete from one of the parents.

(ii) <u>B. 418. 4x Kilimanjaro X McNeil s.n. 4x S. Africa.</u>

AB. 521.A.	71	II	+	2	I.	(2 cells)
	70	II	+	4	I.	(fig. 56)

good spores with negligible abortion.

(iii) B. 418. 4x Kilimanjaro X K.100. 4x Cameroons.

AB. 333.B.	63	II	+	18	I.
	51	II	+	42	I.
AB. 333.C.	68	II	+	8	I.
	67	II	+	10	I.

Although these plants produce about 50% good spores, there is also considerable abortion present, which might be expected particularly with regard to B. 333.B. where 18 - 42 univalents has been observed at meiosis. Spore samples sown have shown some germination.

(iv) B. 448.B. 4x Aberdares X K.100. 4x Cameroons.

AB. 396.A.	70	II	+	4	I.	
AB. 396.B.	71	II	+	4	I.	
	69	II	+	7	I.	
	68	II	+	10	I.	(2 cells)
AB. 397.C.	65	II	+	14	I.	

Spores are mainly good but some fronds have also shown a considerable number of aborted spores.

(v) B. 448.B. 4x Aberdares X McNeil, s.n. 4x S. Africa.

AB. 369.A.	71	II	+	2	I.
	70	II	+	4	I.
AB. 451.C.	72	II			
	71	II	+	2	I.

Good spores.

(vi) B. 418. 4x Kilimanjaro X B. 366.G. 4x Kilimanjaro.

AB. 264.A.	71	II	+	2	I.	
	64	II	+	16	I.	
AB. 264.B.	71	II	+	2	I.	(3 cells)

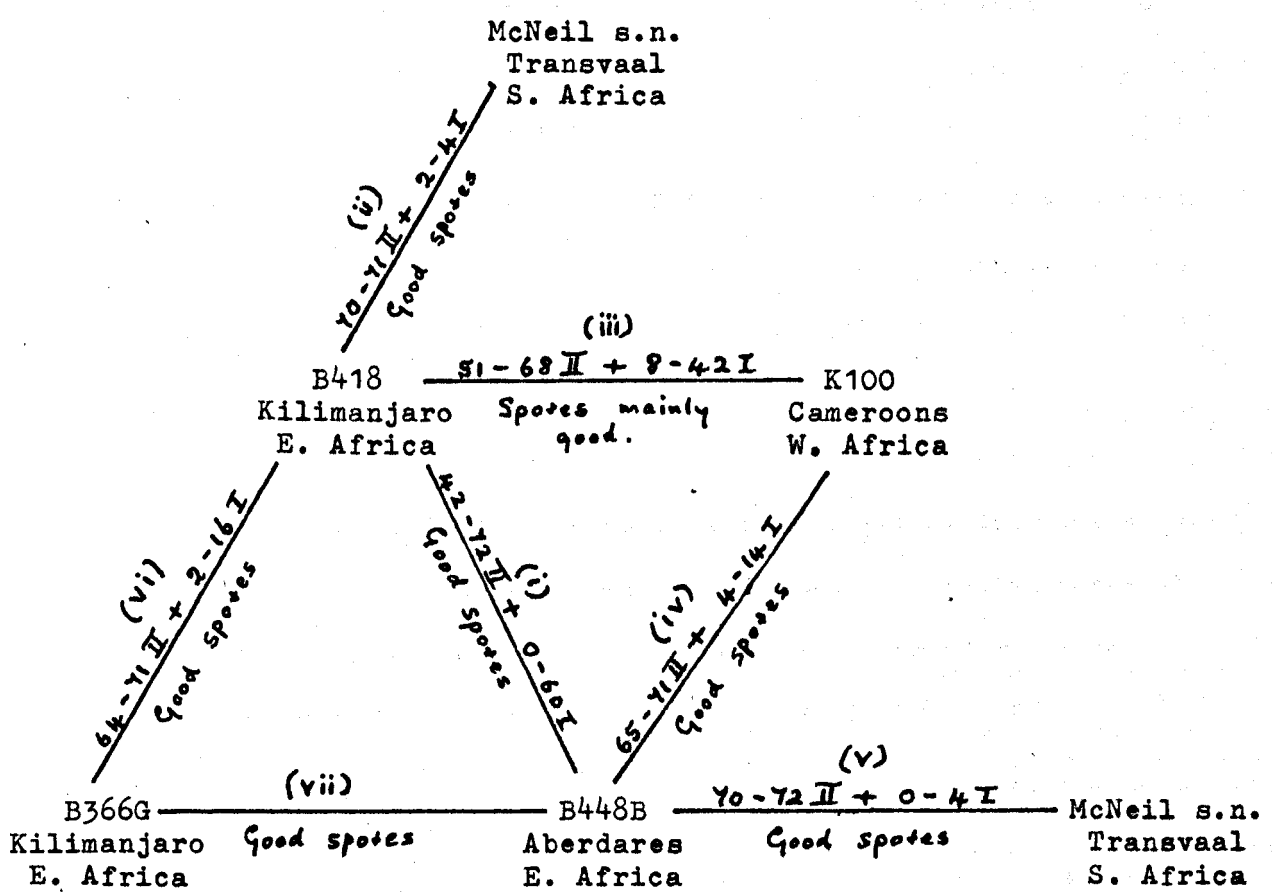
Good spores and those from AB. 264.B. have germinated and the prothalli have given rise to young sporophytes.

(vii) B. 366.G. 4x Kilimanjaro X B. 448.B. 4x Aberdares.

AB. 324.B. No cytological examination of this plant has yet been undertaken but the spores are almost all good.

Summary and Interpretation.

The results from the tetraploid hybrids may be summarised thus:



Although the chromosome pairing at meiosis varies considerably in some of the crosses examined it is thought that those analyses showing maximum pairing are the most significant: since the amount of chromosome pairing potentially possible gives a more accurate indication of the homologies existing between the chromosomes of the plants concerned. Thus the complete or virtually complete pairing observed in the tetraploid crosses suggests that sufficient synaptic homology exists between the 72 chromosomes contributed by each parent to enable them to pair almost completely in the hybrids.

There is, therefore, little cytological evidence from the maximum of 69 or more bivalents observed for all the tetraploid crosses, to indicate any differentiation among the tetraploids. The variation in the number of bivalents seen in some hybrids coupled with the presence of some univalents and loosely associated bivalents in almost all cases, may suggest difficulties in pairing which have arisen through some differentiation between the chromosomes of the various tetraploids used. It may be noted here that loosely associated bivalents and occasionally univalents have been noted in the parents of tetraploid hybrids.

More convincing evidence for some differentiation between two of the tetraploids is perhaps provided by the hexaploid hybrid (ia above) which arose, as a result of an unreduced gamete, during the synthesis of tetraploid hybrids between B. 418 and B. 448.B. The two parental sets of chromosomes are capable of almost complete pairing in the tetraploid hybrids (no. i, above) but when one of these sets is duplicated as in the hexaploid hybrid, the other can only pair with it

partially as shown by the analyses of 75 - 77 associations and 56 - 60 univalents (instead of 72 trivalents that might otherwise have been expected). This must mean either that there is some genetical factor actively suppressing multivalent formation as such, or else that there is preferential pairing between the autosyndetic partners derived from the unreduced gamete and little pairing of any other kind. This is thus possible though not certain evidence for some degree of cytological dissimilarity between chromosomes of B. 418 and B. 448.B.

Apart from the unexpected hexaploid, the univalents are not generally sufficient to prevent the tetraploid hybrids from producing high proportions of good spores. The samples of spores sown have germinated and the prothalli have given rise to young sporelings after self-fertilisation. There has, however, not been sufficient time to fulfill the final criterion for interfertility, of raising a fertile F.2 generation from these hybrids.

HEXAPLOID HYBRIDS.

Thirteen hybrids of this constitution are available involving four of the tetraploids used in the previous section combined with five octoploids, one of these being A. demerkense. The morphology of some of these hybrids is illustrated in fig. 57, 58 and that of two hybrids involving A. demerkense (nos.xix, xx) in fig. 59.

(viii) Hambler 211. 8x W. Africa X K.100. 4x Cameroons.

AB. 307.B.	69	II	+	77 - 78	I.	(2 cells)
AB. 330.	68	II	+	75	I.	
	62	II	+	92	I.	
	61	II	+	94	I.	

(ix) Hambler 211. 8x W. Africa X B. 418. 4x Kilimanjaro.

AB. 376.B.	69	II	+	77	I.	

(x) Hambler 211. 8x W. Africa X B. 448.B. 4x Aberdares.

AB. 519.A.	70	II	+	77	I.	
	67	Associations	+	74	I.	

(xi) Hambler 211. 8x W. Africa X McNeil. 4x S. Africa.

AB. 127.	71	Associations	+	68	I.	(fig. 60)
AB. 420.	70	II	+	74	I.	

(xii) 8x Kenya X K.100 4x Cameroons.

AB. 223.	62	Associations	+	82	I.	(fig. 61)
	60	"	+	91	I.	
	58	"	+	96	I.	

(xiii) 8x Kenya X B.448.B. 4x Aberdares.

AB. 319 B.	69	II	+	78	I.
AB. 362.	72	II	+	72	I.

(xiv) 8x Kenya X McNeil, s.n. 4x S. Africa.

AB. 7.	74	associations	+	57	I.	(fig. 62)
	76	"	+	61	I.	
	73	"	+	68	I.	
AB. 103.E.	73	"	+	66	I.	
	71	"	+	65	I.	

(xv) Schelpe 4281. 8x Knysna X McNeil, s.n. 4x S. Africa.

AB. 109.B.	72	associations	+	65	I.
AB. 110.	74	"	+	63	I.
AB. 126.	77	"	+	51	I.
	74	"	+	64	I.

(xvi) B. 263. 8x Cape X B. 418. 4x Kilimanjaro.

AB. 553.A.	75	associations	+	55	I.
	74	"	+	58	I.
	66	"	+	76	I.

One hybrid of this combination is octoploid.

AB. 553.B.	116 associations	+	50 I.	(fig. 63)
	118 "	+	45 I.	

This octoploid plant produces approximately 50% spores of morphologically good appearance but nothing is known yet regarding their viability.

(silhouettes of both the hexaploid and octoploid plant are shown in fig. 58).

(xvii) B. 263. 8x Cape X B.448.B. 4x Aberdares.

AB. 552.A.	74 associations	+	57 I.
AB. 552.B.	77 "	+	54 I.
	76 "	+	54 I.
	75 "	+	56 I.

(xviii) B. 263. 8x Cape X McNeil, s.n. 4x S. Africa.

AB. 507.C.	74 associations	+	63 I.
AB. 508.C.	74 "	+	63 I.
	73 "	+	66 I.

(xix) A. demerkense 8x 379 X B.418. 4x Kilimanjaro.

AB. 291.A.	76 associations	+	50 I.
	75 "	+	51 I.

Spores abortive.

(xx) A. demerkense 8x B.379 X B. 366G 4x Kilimanjaro.

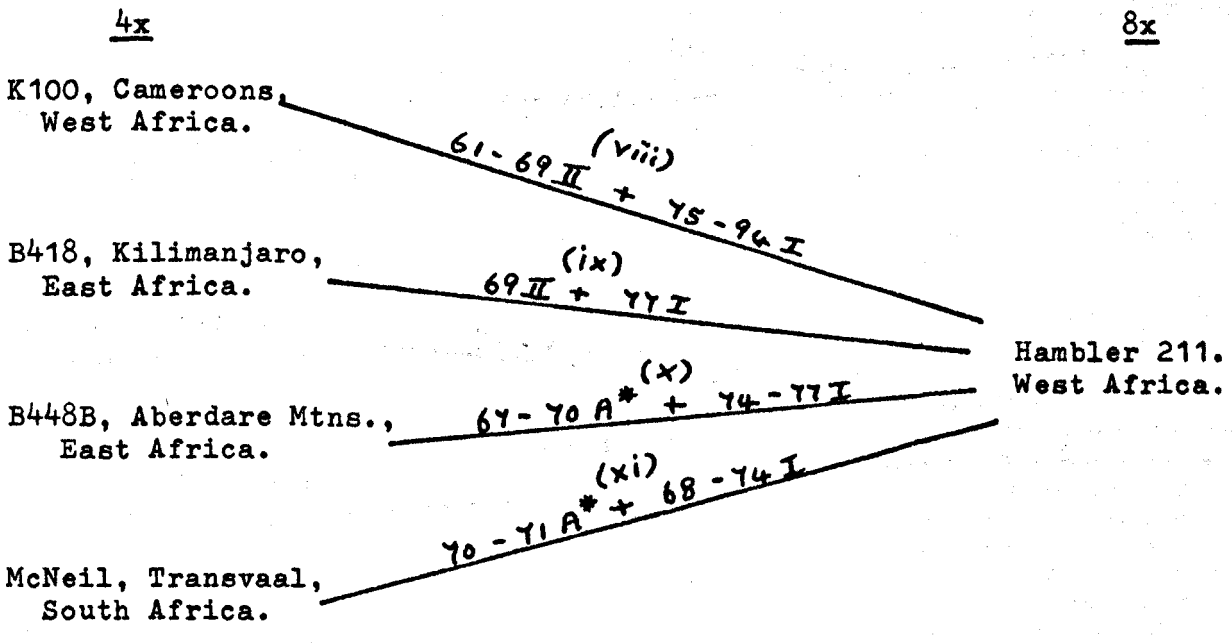
Two hybrids of this combination which have been cytologically examined are both octoploid.

AB. 334A.	130 II	+	24 I.
	129 II	+	30 I.
	129 II	+	30 I.
AB. 305B.	121 II	+	45 I. (very approx.)

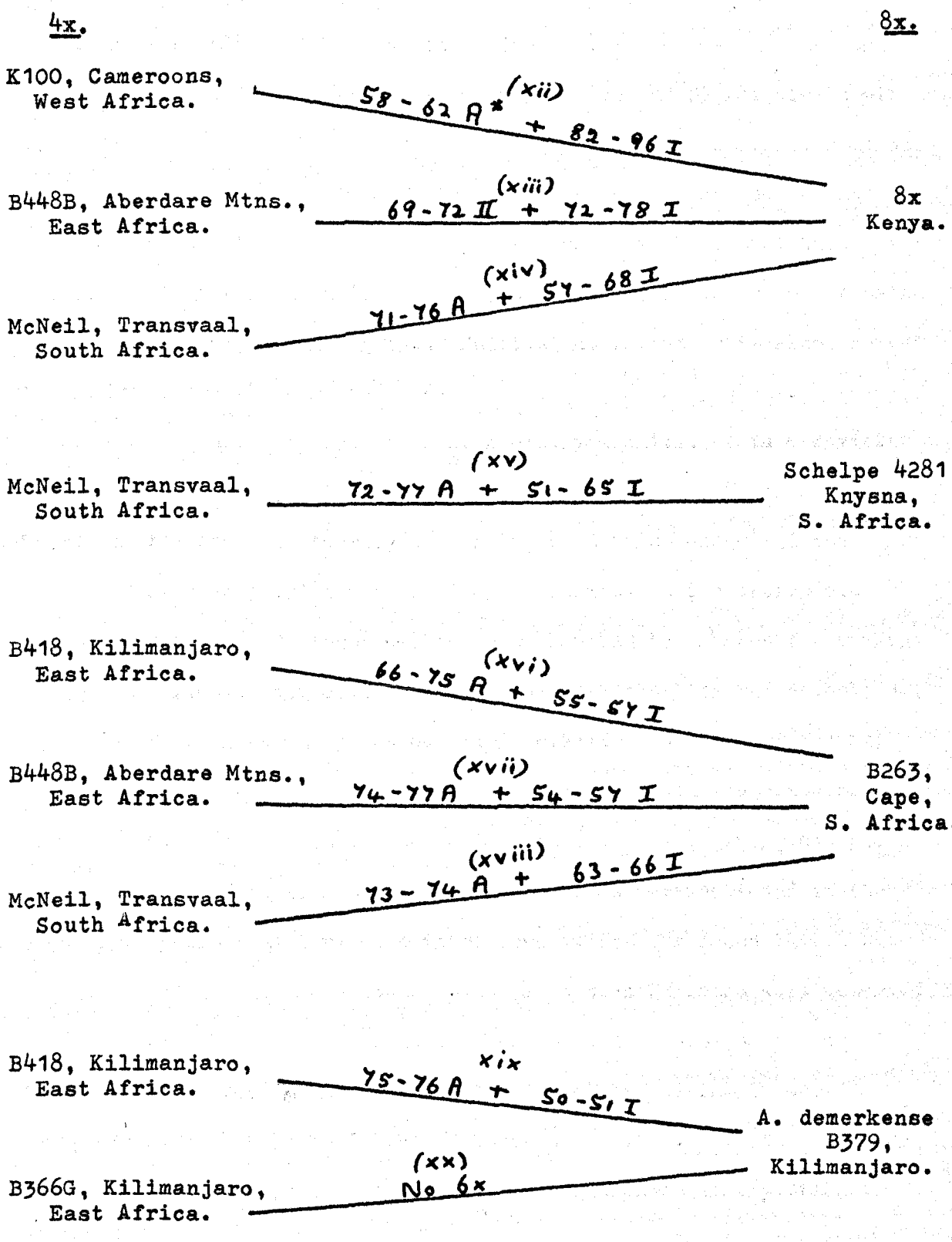
Both plants produce over 50% good spores and those from AB 334A have germinated and the prothalli are producing young sporophytes.

Summary and Interpretation.

Excluding the rather special cases of the octoploids all the hexaploid hybrids just dealt with above show abortive sporangia and aborted spores and the analyses of chromosome pairing are summarised below.



* A = bivalents + multivalents



* A = bivalents + multivalents

These results do not lend themselves to precise generalisations though on the whole they approximate to 72 pairs and 72 univalents with minor divergences in the direction of slightly more than 72 associations in crosses xiv, xv and xvii or slightly fewer in most of the remainder. Where fewer than 72 univalents are present some of the associations are multivalent though their numbers (as indicated by chromosome totals, see p. 62) are usually not great. Multivalent formation is also present in one hybrid (xii) where more than 72 univalents are present. These discrepancies, however, are probably scarcely significant in a phyletic discussion when dealing in numbers as high as 72 and with small samples. Therefore the broad uniformity of chromosome pairing among all the hexaploid hybrids coupled with similar uniformity in the tetraploid hybrids makes these analyses of less use than had been hoped for working out the precise mutual relationships between tetraploids and octoploids.

The special cases of the octoploid hybrids (crosses xvi and xx) deserve special attention since these again involve the functioning of unreduced gametes from the tetraploid parents used, giving octoploid instead of hexaploid plants. In the chromosome pairing found in these plants, 72 pairs will have been introduced by the unreduced gamete but the fact that in each case considerably more than 72 pairs were observed indicates clearly that a considerable capacity for autosyndesis exists in both octoploids. This fact together with the pairing in the hexaploid hybrids will be further discussed on p.112. In the meantime it is sufficient to point out the need for caution in interpreting the facts on too narrow a basis.

OCTOPLOID HYBRIDS. (8x X 8x).

Results are available from six hybrids of this composition involving 5 different octoploids, one of which is A. demerkense. This morphology (except that for no. xxiii) is illustrated in figs. 64, 65.

(xxi) Hambler 211. 8x W. Africa X 8x Kenya.

AB. 536.A.	143	II	+	2 I.	(fig. 66)
	138	II	+	12 I.	
AB. 536.B.	141	II	+	4 - 6 I.	(2 cells)

Good viable spores.

(xxii) Hambler 211. 8x W. Africa X B. 263. 8x Cape.

AB. 479.D.	143	II	+	2 I.
	140	II	+	8 I.

Good spores which on sowing have germinated.

(xxiii) Hambler 211. 8x W. Africa X Schelpe 4281. 8x Knysna.

AB. 513.A. This plant shows almost complete pairing of the chromosomes at meiosis but no accurate analysis has been possible. This observation is further supported by the fact that the plant produces good spores.

(xxiv) A. demerkense 8x B. 379. X Hambler 211. 8x W. Africa.

AB. 570.A.	99	associations	+	87	I. (fig. 67)
	110	"	+	66	I.
AB. 569.A.	107	"	+	60	I.

Spores abortive.

(xxv) A. demerkense 8x B. 379. X Schelpe 4281. 8x Knysna.

AB. 517.A.	113	associations	+	33	I.

Spores abortive.

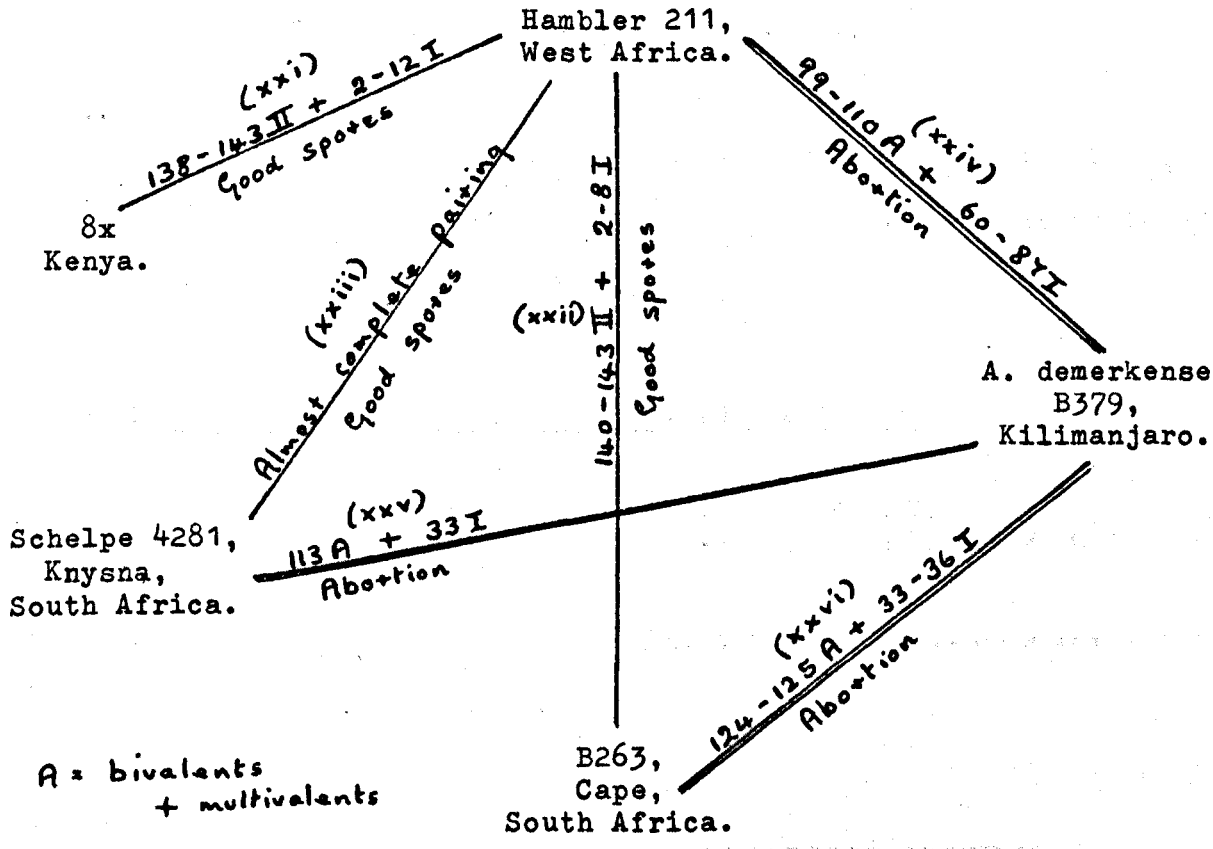
(xxvi) A. demerkense 8x B.379. X B. 263 8x Cape.

AB. 562.B.	125	associations	+	36	I.
	124	"	+	33	I.

Spores abortive.

Summary and Interpretation.

The chromosome pairing at meiosis in this group of hybrids is summarised diagramatically below.



The striking feature of these octoploid hybrids is the regular meiosis in the crosses between the A. aethiopicum octoploids and the meiotic irregularity characterising the hybrids between them and A. demerkense (nos. xxii, xxiii and xxiv). The two types of meiotic behaviour are reflected in good spore production and probable interfertility in the A. aethiopicum hybrids and the almost wholly abortive spores in the hybrids involving A. demerkense. This suggests that alone among all the forms quoted so far in the hybridisation programme A. demerkense may perhaps rightly be referred to a different taxon.

OCTOPLOID HYBRIDS. (12x X 4x).

Hybrids certainly of this composition are limited to two but several others have been synthesised but are still too young to quote. The two hybrids are illustrated in fig. 68.

(xxvii) Manton, s.n. 12x Madeira X K.100 4x Cameroons.

AB. 206.B.	122 associations	+	41 I.	
	119 "	+	45 I.	(fig. 69)

The spores are largely abortive but the plant produces a few of morphologically good appearance.

(xxviii) B. 128. 12x S. Africa X McNeil, s.n. 4x S. Africa.

AB. 523.B.	105 associations	+	70 I.
	104 "	+	73 I.

Spores completely abortive.

Interpretation.

Assuming the maximum pairing possible by allosyndesis in these two hybrids there is clearly a minimum of 47 - 50 bivalents in the first (xxvii) and 32 - 33 in the second (xxviii) being formed by autosyndesis of chromosomes contributed by the dodecaploid parents.

In addition the first hybrid (xxvii) demonstrates some unequivocal allosyndesis as the number of associations observed at meiosis is greater than the number that could be formed even by complete autosyndesis of the chromosomes from the dodecaploid parent, i.e. greater than 108 bivalents.

Other 12x X 4x hybrids.

Four additional hybrids intended to be of this composition have turned out to be decaploid instead of octoploid. In each case the morphology as well as the chromosome number indicates the participation of an unreduced gamete from the tetraploid. Each of these hybrids is highly sterile, producing only abortive spores.

The parentage of the four hybrids is as follows:-

(xxix) AB.361.A. Manton, s.n. 12x Madeira X B.448.B. 4x Aberdares.
(xxx) AB.361.C. " " " X " "
(xxxi) AB.259.A. Manton, s.n. 12x Madeira X B.418 4x Kilimanjaro.
(xxxii)AB.259.B. " " " X " "

Accurate analyses of chromosome pairing in these hybrids has not been attempted but a cell from one of them (xxxi) is illustrated in fig. 70 to show the sort of evidence available for establishment of ploidy. It shows approximately 120 associations and 101 univalents representing a chromosome total of at least 341. (Decaploid 2n = 360). Other cells with more associations and fewer univalents have recently been obtained from the same plant. The other three are also showing a similar increase of chromosome pairing so that no conclusions will at present be based on the analyses so far available, but the hybrids are mentioned as additional evidence for the functioning of unreduced gametes in the breeding programme.

DECAPLOID HYBRIDS. (12x X 8x).

Many decaploid hybrids have been synthesised, by crossing the octoploids with the three dodecaploid plants available, as shown in the hybridisation diagram on p. 60. These hybrids will not be enumerated in detail here since this combination had already been studied to some extent by Panigrahi (Thesis 1954) and time has not permitted this part of the work to be extended further. However it may be noted that so far without exception those hybrids of this combination which have become mature are all sterile, producing abortive spores.

DODECAPLOID HYBRIDS.

Three dodecaploid hybrids synthesised between the three 12 ploid stock plants, have been studied. Fronds from two of these hybrids are shown in fig. 71.

(xxxiii) Kerr 137. 12x St. Helena X Manton, s.n. 12x Madeira.

AB. 442.A. Meiosis irregular with some multivalent formation and two cells have shown approximately 50 - 54 univalents each.

Spores abortive.

(xxxiv) B. 128. 12x S. Africa X Manton, s.n. 12x Madeira.

AB. 453.A. Meiosis irregular. Cells seen with 50 - 54 univalents.

Spores abortive.

(xxxv) B. 128. 12x S. Africa X Kerr 137. 12x St. Helena.

AB. 635.A. Spores abortive.

AB. 635.B. Spores abortive.

Interpretation.

The sterility of these hybrids suggests some genuine cytogenetic differentiation between the dodecaploid parents. The interpretation to

be put upon the limited number of univalents observed at meosis in two of the hybrids is not immediately ascertainable so that the exact nature of the differentiation is unknown.

V. STERILE WILD PLANTS.

Before dealing with the apogamous section of the complex the study of the sexual populations will be completed with examination of the evidence for natural hybridisation.

While measuring spores taken from herbarium material it was observed that a number of specimens showed either only abortive spores or completely aborted sporangia. Although such sterility was indicative of natural hybridisation no cytological evidence was available at the time for natural hybrids. However plants collected from localities where bad spore production had previously been noted have subsequently been shown to possess irregular meiosis, typical of that already seen in artificial hexaploid hybrids. These sterile plants are often easily picked out in the field and on herbarium sheets because they frequently possess light orange-brown coloured sori caused by the abortive sporangia, which contrasts with the darker brown sori of fertile plants. Whilst the evidence strongly indicates a hybrid origin for some of these plants, this is not so for others for reasons explained below.

Nearly all the plants to be dealt with in this chapter are hexaploid and it has already been noted from the artificial hybridisation programme that sterile hexaploids can be produced in two different ways. Firstly by crossing the tetraploid and octoploid cytotypes and secondly by hybridising two tetraploids one of which produces an unreduced gamete (hybrid i.a. p. 64). There seems little reason why the latter should not occasionally occur within a wild tetraploid population, and therefore considerable caution is indicated in suggesting the origin of two of the

sterile plants to be quoted.

As with the artificial hybrids detailed presentation in this chapter will be limited to those plants where some analysis of chromosome pairing at meiosis has been possible. It is felt that these examples will be more illuminating if presented against the background of their locality, which will be used as a heading in each case.

a) Ceylon Forest Reserve, Transvaal, South Africa.

Around a waterfall in this locality considerable quantities of the S. African tetraploid A. aethiopicum var tripinnatum Baker were found growing generally on the forest floor. Just below the fall a large boulder protruding over the stream was covered with the tetraploid (fig. 72a) and on the outer edge in almost full sun were a few plants (probably a small clone) showing abortive spores. One of these, B. 159 (fig. 72b), has been subsequently shown to be hexaploid and therefore potentially of a hybrid origin, although no other cytotypes were seen in the vicinity.

A cell from the plant from which the hexaploid level of ploidy was established showed approximately 72 bivalents and 72 univalents at meiosis. Later preparations from the same plant yielded poorer cells but provide strong evidence that the amount of chromosome pairing can increase appreciably. Accurate analyses of all these cells has not been possible but two of them show in the region of 72 or slightly more associations and a maximum of 50 univalents. There is clearly increased multivalent formation in the later cells which accounts for the decrease in unpaired bodies. This suggests some homologies

between the three sets of 72 chromosomes present in the plant.

This sterile plant is morphologically similar to the one to be dealt with next and as both have been found in somewhat similar circumstances their possible origin will be discussed together at the end of the next subsection.

b) Kowyn's Pass, Graskop, Transvaal.

This locality is a forested pass on the Great Escarpment of the Eastern Transvaal where the South African tetraploid grows abundantly in the more open forest near the top. Slightly lower in denser forest a small epiphytic sporeling was collected. This sporeling (B. 235) has been raised to maturity in cultivation and worked cytologically. The spores are wholly abortive except for odd ones of good appearance. Again as in the previous case no octoploid was found in the locality.

Meiosis is irregular and a cell is illustrated in fig. 73 which immediately shows the difficulties involved in analysing such cells. It is not easy in this case to demonstrate the grade of ploidy clearly but the plant is almost certainly hexaploid and the cell shows approximately 71 associations and 25 univalents. There are numerous large and peculiarly shaped chromosome bodies in the cell in fig. 73 which suggests that a considerable number of the associations are multivalent thus accounting for the low number of univalents observed.

. . . . . .

The two sterile plants just dealt with are morphologically similar when in cultivation and their chromosome number immediately suggests that both have arisen by the combination of the tetraploid and an octoploid. Although the octoploid cytotype was not found in either locality this cannot be used as evidence against a hybrid origin of the two plants as failure to find an octoploid may only imply its rarity and not complete absence. However even if it is completely absent from both localities, spores of octoploids from other localities could settle and occasional hybrids with the tetraploid arise in this way.

On the other hand their solitary nature in a tetraploid population could also mean that the two sterile plants have arisen by the less obvious method of the addition of a normal and unreduced gamete from the tetraploid. This would produce an autopolyploid. Signs of autopolyploidy are manifest in both the hexaploids particularly in the one from Kowyn's Pass (B. 235). Similar chromosome pairing could however conceivably arise if an autooctoploid was backcrossed with its tetraploid progenitor so that on cytological grounds it would not generally be possible to differentiate hexaploids arising in the two different ways.

The morphological evidence for either of the two alternative modes of origin is similarly not conclusive. The sterile plant B. 159 from the Ceylon Forest Reserve and the tetraploid growing with it are shown in fig. 72 and differences mainly of a quantitative nature may be seen between them. The frond of the sterile plant is less dissected than the tetraploid with generally larger, less dissected pinnules and fewer

reduced pinnae at the base of the lamina. These characters may represent an intermediate condition between the tetraploid var Tripinnatum Baker and an octoploid such as that known from the Transvaal (fig. 35). However some evidence was presented earlier to suggest that a rise in ploidy is reflected in less dissected fronds (see p.21) so that the question arises as to whether the addition of a normal and unreduced gamete of the tetraploid could produce the differences already noted between the sterile plants and the tetraploids.

It is therefore not possible until further studies have been completed on these two sterile plants and their postulated progenitors to be certain of their origin.

c) Woodbush, Transvaal and Swaartkop, Natal.

Two other plants from S. Africa have been shown to possess irregular meiosis and are sterile. Both are thought to be of hybrid origin but the cytological information on chromosome number and pairing is not complete.

AB. 254.B. Woodbush, Transvaal, Irregular meiosis and probably hexaploid.

This fern is very similar to the plants dealt with in a) and b) but is slightly larger and more vigorous. It is thought to have arisen by the hybridisation of the tetraploid and octoploid cytotypes, both present in this locality. The tetraploid is of the var tripinnatum Baker type which was frequently found growing terrestrially, while the octoploid was occasional and epiphytic, often at a considerable distance from the forest floor. The hybrid was again epiphytic but

more frequent and obvious than the octoploid and easily distinguished from the latter by its larger size and orange brown sori.

AB. 271. Swaartkop, Natal. Irregular meiosis, probably hexaploid.

Tetraploid and octoploid cytotypes are both present in this locality (as indicated by spore measurements) and the sterile plant has probably arisen between them. The ecological pattern was identical to that at Woodbush above although the suspected hybrids were less frequent but nevertheless very noticeable.

d) Kumugu River, Kericho, Kenya.

The most fully documented, both morphologically and cytologically, example of natural hybridity within the complex is illustrated by two hybrids and their parents from Kericho in Kenya. The neighbourhood is a tea growing area and the locality consisted of some virgin forest, lining the banks of the Kumugu River just behind the Tea Hotel at Kericho, which has escaped clearance for plantation presumably because of its topographical unsuitability.

In the forest a tetraploid of the less dissected East African group (p. 37) and two octoploids were discovered. The two latter in this locality were reasonably distinct, one being small and epiphytic with spores possessing a shallow inconspicuous perispore wing (B. 484; silhouette, fig. 36; spores, fig. 40d) and the other larger and terrestrial with spores showing broader and more conspicuous perispore wings (B. 485; silhouette, fig. 37; spores, fig. 40c). The tetraploid (B. 487, fig. 27) was also terrestrial and growing on the river bank close to the larger octoploid.

Intermingled with the few tetraploid plants were two very vigorous sterile specimens (B. 489-90), their orange sori contrasting strongly with the almost black sori of the tetraploid. Further, though smaller, sterile plants were collected from the trees among the not too frequent epiphytic octoploid. These epiphytic sterile plants (B. 483) were easily distinguished from the epiphytic octoploid by their larger size, lighter coloured sori and markedly pendulous habit. Similar epiphytic sterile plants were very common in one part of the forest, where the lower horizontal branches of many trees were thickly covered. The plants on each branch may well represent clones derived from one or two original plants, by branching of the rhizome.

Representatives from the two groups of sterile plants have been found to be hexaploid and analyses of chromosome pairing at meiosis for an example from each group are given below:

B. 490. approx. 72 II + 72 I. (2 cells).

B. 483. approx. 69 associations + 43 I.

The three fertile cytotypes in this locality are distinct enough morphologically to propose that the sterile plants are hybrids which have arisen between the tetraploid and two octoploids as set out in fig. 74. In this figure only comparable pinnae are illustrated but the arrangement is substantiated by a study of frond size, shape and texture.

It has not yet been possible to check the consistency of the chromosome pairing in the two hybrids. However on the basis of the

results available the multivalent formation evident in the hybrid (B. 483) between the tetraploid and smaller epiphytic octoploid suggests this octoploid to be capable of some unequivocal autosyndesis. Similar autosyndesis is not shown for the larger terrestrial octoploid as the 72 bivalents and 72 univalents observed in the hybrid between it and the same tetraploid could all have arisen, though not certainly, by pairing of the chromosomes contributed by the tetraploid with half of those of the octoploid. There is therefore from these two hexaploid hybrids involving the one tetraploid and two octoploids in this locality evidence to suggest some cytological difference between the two octoploids.

This example has provided the most spectacular evidence of natural hybridisation between different ploidies, the epiphytic hybrids being much more frequent than either of their parents, although this may have been partially caused by plants producing clones as suggested earlier. It seems possible that the clearance of the surrounding forest for tea plantations, which must have altered the environment in the forest remaining to some extent, has been responsible for this burst of hybridity.

e) Other sterile plants.

Two sterile plants have been collected which have proved difficult to work cytologically and only very approximate analyses of chromosome pairing at meiosis have so far been obtained. These do, however, strongly indicate that both plants are octoploid, chromosome counts always being considerably in excess of the hexaploid number but approaching the octoploid number. In the absence of any accurate analyses no attempt will be made to explain their origin but they are being mentioned to show that sterility in the wild is not exclusive to the hexaploid

level of ploidy which might be suggested by the rest of this chapter. The localities of the two plants are as follows:

B. 100. Meiring's Poort, Oudtshoorn Div. Cape, S. Africa.

B. 314. Lushoto, Usanbara Mtns., Tanganyika.

. . . . . .

The four sterile hexaploid plants from Woodbush, Swaartkop and Kericho (subsections c and d) are almost certainly of hybrid origin having been synthesised from the tetraploid and octoploid cytotypes present in these localities. The evidence, however, for a similar origin of the two sterile plants from South Africa dealt with in subsections a) and b) is less certain.

The cytological information (apart from the establishment of ploidy) for the four hybrids is not complete but where information on chromosome pairing at meiosis is available the results resemble those from artificial hexaploid hybrids (see p. 72), particularly in the number of bivalents or associations.

In addition to the four established live hybrids studied, situations have been revealed during herbarium studies in material from other parts of Africa where sterile specimens have been collected from localities where the tetraploid and octoploid cytotypes (as indicated by spore measurements) are also present. Consequently from my own personal field experience and herbarium studies it does not seem too optimistic to state that sterile hexaploid hybrids frequently arise whenever tetraploids and octoploids grow in close proximity.

VI. APOGAMOUS FORMS.

In addition to the sexual populations dealt with in the previous chapters, apogamy of a somewhat unusual type has been encountered sufficiently often to justify special treatment in a separate chapter. The sporangial development in these apogamous forms differs from that previously described for other apogamous ferns (Dopp, 1932; Manton, 1950) in starting with 16 spore mother cells and ending with 16 diads of spores. The cytological peculiarities can be dealt with briefly since they have already been described in a paper (Braithwaite, 1964, in the press), which can be summarised as follows.

The spore mother cells arise in the usual way following four successive mitotic cleavages of the archesporium. At meiosis the mother cells show no trace of chromosome pairing, univalents in a range of ploidies being encountered at diakinesis and metaphase I (see figs. 75 , 76 , 78 - 90). The first metaphase is marked by division figures of an irregular appearance (figs. 75 , 76) but eventually all the univalents lie in the equatorial plane of the spindle (fig. 76) where they form a restitution nucleus (figs. 75 , 76). After a period of rest of unknown duration the restitution nuclei undergo what at first sight could be mistaken for a simple mitotic division. Except for the presence of only one spindle the chromosome behaviour is however that of a typical second meiotic division. The metaphase chromosomes now manifestly double (fig. 77) from a very regular metaphase plate (fig. 75) and at anaphase the constituent chromatids move to opposite poles (fig. 75) forming two nuclei at telophase. The cytoplasm finally cleaves to produce

diads (figs. 75., 77).

Every sporangium is therefore capable of producing 32 spores containing the same number of chromosomes as appeared in the spore mother cells at diakinesis. Thus the inherent requirement of apogamous ferns for an unreduced chromosome complement in the spore, to compensate for the absence of sexual reproduction in the prothallus, is satisfied.

The diads yield spores of a rather characteristic rounded shape which is generally easily picked out in spore mounts and has been found useful in separating the apogamous forms from the sexual members of the complex (see p.22).

A proportion of sporangia abort completely in both wild and cultivated plants. In addition spore counts from other sporangia indicate that the theoretical maximum of 32 spores per sporangium is not always attained, 'good' sporangia yielding anything from 23 - 32 spores and occasionally less. This may be partially explained by a residual tendency for the mother cells to cleave into triads or tetrads at the end of the division. When these cytoplasmic activities interfere with one or both of the telophase nuclei the resulting spores will probably be abortive. Often, however, these abnormal cleavages result in a diad with two small portions of cytoplasm cut off on either side without nuclear material. These latter probably do not seriously affect either the viability or appearance of the mature spores.

The apogamous development of prothalli has been watched but displays nothing remarkable. The prothalli do however show poor

antheridial production (see p.8) and the lack of active spermatozoids has made it impossible to incorporate any of the apogamous plants into hybrid combinations with sexual plants.

A list of apogamous plants is assembled in Table I with their chromosome numbers and grade of ploidy in the last two columns, except for two plants (Mitchell 479 and Kunkel 6722) which are still too young for cytological analysis. Cells from Mitchell 88, Braithwaite 228 and Braithwaite 103.A are shown in figs. 78a, 79a, 80a respectively and explanatory diagrams for these cells in the same order in figs. 78b, 79b, 80b.

TABLE I.

Details of source, locality and cytological data for the live material of the apogamous section of the A. aethiopicum complex.

Collector	Locality	Chromosome No.	Ploidy
Curle & Schelpe 1. (live plant)	Dessie Rd., nr. Addis Ababa, Ethiopia.	2n = c. 288	8x
Nash 183. (spores)	Musitu, Abercon Dist., Northern Rhodesia.	2n = c. 288	8x
Mitchell 88. (live plant)	Dombashawa, nr. Salisbury, Southern Rhodesia.	2n = 288.	8x
Mitchell 479. (spores)	Chinamora Reserve, nr. Salisbury, S. Rhodesia.	- - -	- -
Williams UMT. 1A (live plant)	Murakwa's Hill, Umtali, S. Rhodesia.	2n = 288	8x
William's UMT. 1B (live plant)	Murakwa's Hill, Umtali, S. Rhodesia.	2n = c. 288.	8x
Braithwaite 222. (live plant)	Pilgrim's Rest, Transvaal, South Africa.	2n = c. 288.	8x
Braithwaite 228. (live plant)	Pilgrim's Rest, Transvaal, South Africa.	2n = 288.	8x
Nat.Herb. Pretoria. "Garst. C" (live plant)	Garstfontein, Pretoria, Transvaal, S. Africa.	2n = 288.	8x
Braithwaite 103A. (live plant)	Nr. Conway, Cape Prov., S. Africa.	2n =c.330-357.	10x
Braithwaite 103B. (live plant)	Nr. Conway, Cape Prov., S. Africa.	2n = c. 346.	10x
Kunkel 6722. (spores)	La Palma, Canary Islands.	- - -	- -

From the chromosome preparations it will be perhaps clear that in spite of very high numbers the absence of pairs permits counts to be made to a high degree of accuracy in most cases. Slight uncertainty caused by overlapping of a few individual chromosomes does not prevent, it is felt, effective establishment of ploidy, but where a recognised element of uncertainty exists, though in no case greater than $\pm$ 8 chromosomes, an approximation sign (c) is put before the count in the Table. In view of the pattern of ploidy already established for sexual members of the complex it seems probable that the majority of plants listed in the Table will have had exactly 288 somatic chromosomes (i.e. the normal octoploid number). Slight deviations would however be difficult to detect and cannot entirely be discounted though they are certainly not great. The two plants from one locality in South Africa (Braithwaite 103A, 103B) giving considerably higher chromosome counts and have been provisionally designated as decaploid.

MORPHOLOGY AND TAXONOMY.

The apogamous section of the complex presents a considerable range of frond morphology so that it is impossible to define any gross morphological characters which would distinguish them all from the sexual forms, although to one familiar with the complex the apogamous plants can often be recognised in some regions without resorting to spore characters. Frond characters may, however, be used to divide the apogamous forms themselves into three broad geographical groups, two of which show considerable uniformity while the third

is more heterogeneous.

The variation in frond morphology will therefore be dealt with in three groups and, as for the sexual plants, correlated with any species previously described.

GROUP I. A.filare (Forsk.) Alston.

in Pteridophyta, in Mr. John Gossweiler's plants from Angola and Portuguese Congo. J. Bot., Lond., 72, Suppl. 2, 1934.

Acrostichum filare Forsk. Fl. AEgyptiaco-Arabica, 184, 1775.

A. canariense Willd. Willd. sp. 5, 339, 1810.

East, North-East and West Africa, Canary Islands.

Description: Rhizome short creeping. Fronds 15 - 35 cm. long but sometimes up to 46 cm. long. Stipe short, 3 - 13 cm. long,densely fibrillose. Lamina, bipinnatifid to bipinnate, lanceolate to narrowly ovate with an acuminate apex, with 8 - 20 pairs of subopposite pinnae the lowermost 4 pairs usually being markedly decrescent. Pinnae, stiff, narrow and acute with long attenuated points, divided into narrow cuneate almost linear lobes although in larger specimens pinnae divided into 1 - 3 distinct pinnules as well as lobes. Pinnules and lobes narrow almost linear with irregularly toothed apices. Rachis and pinnae markedly fibrillose on all surfaces. Sori when mature may coalesce to form a continuous mass of ripe sporangia on the under-surface of the pinnae. Spores globose with a broad cristate perispore wing.

(Two silhouettes of fresh fronds from a live plant from Ethiopia are illustrated in fig. 81 and spores are shown in fig. 84a.)

GROUP II. A. aethiopicum s.l.

Northern and Southern Rhodesia, Mozambique, Nyasaland and Angola.

Description: Rhizome short creeping. Fronds bipinnate to tripinnate, 25 - 30 cm. long. Stipe 11 - 20 cm. long and fairly densely covered in a reddish-brown tomentum. Lamina 18 - 30 cm. long and 9 - 18 cm. broad, deltoid to narrowly deltoid, the lowermost pairs of pinnae rarely being reduced. Pinnae, spreading and obtuse, and divided into as many as 4 - 6 distinct pinnules and a number of lobes tapering to a point. Pinnules, broad, cuneate and further divided into 3 or 4 lobes or in larger specimens 1 or 2 distinct segents and 2 or 3 lobes. Apices of all ultimate segments and lobes irregularly serrate. Rachis densely fibrillose and the undersurface of the pinnae less so. Spores globose with a conspicuous cristate perispore wing.

(silhouettes of fresh fronds are illustrated in fig. 82, and spores in fig. 84b).

This group may be distinguished from A. filare by :-

1) Narrowly deltoid to deltoid fronds.
2) Less acute pinnae without long attenuate points.
3) Broader and more divided pinnules.

GROUP III. A. aethiopicum s.l.

S. Africa.

Description: Rhizome creeping. Fronds 20 - 50 cm. long and densely fibrillose on the stipe and rachis. Lamina, bipinnatifid to tripinnatifid, 15 - 35 cm. long and 5 - 14 cm. wide, lanceolate to narrowly ovate with sometimes a short acuminate apex. Fronds with 10 - 20 pairs of subopposite pinnae, the lowermost 3 or 4 pairs being usually slightly reduced but sometimes markedly decrescent. Pinnae either narrow and acute with attenuate point and cut into lobes or are broader without less attenuated point and cut into 4 - 5 distinct pinnules. Pinnules divided again into 2 - 4 lobes. All ultimate lobes of pinnae with irregularly furcate teeth or serrate at their apices. Spores globose with cristate perispore wing.

(silhouettes of fronds from a number of South African apogamous plants are assembled in fig. 83 and spores are illustrated in fig. 84c).

This is rather a heterogeneous group which is difficult to describe adequately and a clearer picture of the variation can probably be obtained from the silhouettes (fig. 83). The two levels of ploidy shown earlier to be present in the South African apogamous material (see Table I, p.95)are responsible for part of this variation. The two decaploid plants (fig. 83, b,d) are smaller with more obtuse and blunt pinnae than the more frequent octoploids. There is, however, considerable variation within the octoploids as can be seen from the

examples illustrated (fig. 83, a,c,e,). The less dissected forms show a number of features in common with A. filare, such as the narrow fronds with acuminate apices and acute and narrow pinnae with attenuate points, but these characters are never so pronounced as in that taxon and the larger more dissected apogamous octoploid illustrated (fig. 83,a) shows little trace of the characters.

DISTRIBUTION AND ECOLOGY.

The distribution of the three groups described in the previous section are shown in fig. 85, that of Group II being enclosed by a broken line. The collections from the northern half of the continent and adjoining Arabia are rather sparse, particularly from the more remote and inaccessible regions, so that the distribution data so far available for these regions are probably far from complete. The localities of personal collections and herbarium specimens show a range of altitude from just over 4000 feet in South Africa to 7-8000 feet in East Africa.

In Africa the apogamous forms cover approximately the same geographical area as sexual members of the complex, but in the southern part of the continent particularly, they are more closely associated ecologically to the sexual dodecaploid cytotype than to either the tetraploids or octoploids. Thus in South Africa they occupy, as did the sexual dodecaploid (see p. 54), drier areas usually towards the interior, away from the forested escarpment in the east favoured by the sexual tetraploids and octoploids. A good illustration of this feature

is seen in the Transvaal where apogamous plants spread westwards onto the central plateau from the rim of the forested escarpment formed by the northern extension of the Drakensberg. Here they are found on rocky outcrops and in small wooded kloofs of the high veldt. Further south in Natal and the Eastern Cape Province apogamous plants tends to grow below the escarpment and the drier areas occupied by these plants is perhaps best illustrated by the decaploid B. 103 which was collected in the Karroo just south of Middleburg. Although in places locally frequent the apogamous material was never seen in great abundance and sometimes a population consisted of only a few solitary individuals.

In Northern and Southern Rhodesia the apogamous plants (Group II) again show a distribution which bears a closer resemblance to that of the suspected sexual dodecaploids than to that of either the sexual tetraploids or octoploids; the two latter being confined almost exclusively to the forested areas at the eastern edge of the central plateau. Notes recorded on herbarium specimens indicate that the apogamous plants frequently grow in rock crevices or on rock shaded by trees in ravines etc. Material of both apogamous and suspected dodecaploid plants has been collected together from two localities in the Rhodesias.

The distribution patterns of apogamous and sexual members of the complex in southern Africa are shown in figs. 86 and 87, which illustrate some of the features already mentioned. The close resemblance of the apomict and sexual dodecaploid distributions is shown in fig. 87, although the Rhodesian apomicts (Group II) extend into Angola well beyond

the range of any suspected dodecaploid cytotype. A comparison of fig. 87 with the distributions of the sexual tetraploids and octoploids in fig. 86a,b, shows that in general the apogamous and sexual dodecaploid plants occupy more central areas than either of the two lower sexual ploidies; the two latter being mainly confined to the eastern edge of the apogamous and dodecaploid distributions. It will also be noted from these maps that the southernmost limit of the apogamous forms in the Eastern Cape Province of South Africa coincides approximately with that of the sexual tetraploid and dodecaploid cytotypes, while the distribution of sexual octoploids continues westwards to the Cape Peninsula.

VII. DISCUSSION.

In attempting to draw conclusions from the data presented so far it will be convenient to consider the apogamous and sexual forms separately before summing up.

Discussion of apogamy and apogamous forms of the A. aethiopicum complex.

It has already been noted that the sporangial development associated with apogamy in the complex differs from that in other apogamous ferns, which has been described independently by Döpp (1932) and Manton (1950). Nevertheless there are some similarities between the two and since the cytological phenomena described in Chapter VI have not previously been recognised in apogamous ferns it will be appropriate to make a brief comparison of the two types of sporangial development now known.

The doubling of the chromosome number required for the formation of diplospores is achieved in both cases by means of restitution nuclei, formed either before or during the meiotic process. These produce two very different types of meiotic appearance. On the one hand (Manton, 1950) meiosis is normal resulting in tetrads of diplospores. This occurs in a sporangium with 8 mother cells following a restitution nucleus at the pre-meiotic mitosis of the archesporium e.g. Pteris cretica, Cyrtomium falcatum, Asplenium monanthes etc. On the other hand a restitution nucleus affecting the first meiotic division in a sporangium with 16 spore mother cells results in an abbreviated meiotic process ending in diads, as described in Chapter VI for A. aethiopicum. In both cases there are 32 spores per sporangium.

The uniform behaviour of each sporangium before meiosis in A. aethiopicum in that 16 spore mother cells are always formed contrasts strongly with the rather complex situation in apogamous ferns hitherto known. In the latter three principal types of sporangia arise with 4, 8 and 16 spore mother cells respectively. Only the eight-celled produce diplospores. Traces of cytoplasmic activity during the abortive telophase of the last archesporial division sometimes results in a fourth type of sporangium exhibiting partial or complete amitotic cleavages of the mother cells. These correspond in a general way with the abnormal cleavages sometimes encountered in A. aethiopicum as described on page 93. A tendency towards amitosis following a restitution nucleus is thus present in both types of apogamy though it is manifested at correspondingly different places in the spore production process.

Although perhaps the abbreviated meiosis observed in the apogamous members of the A. aethiopicum complex is uncommon among ferns a similar meiotic process has been known in apomictic flowering plants for a considerable time (Gustafsson, 1946, 1947). It has been described in both the Taraxacum and Antennaria types of diplosporous embryo sac formation and as male meiosis in Taraxacum boreale amongst others. Gustafsson refers to this type of meiosis as a "restitution nucleus together with a pseudohomeotypic division" and it is generally preceded by complete asynapsis.

There is some evidence in the literature to suggest that similar cytological phenomena may also be present in other apogamous ferns. Mehra and Singh (1957) found in meiosis of Trichomanes insigne v.d.B forma β from the Darjeeling Himalayas complete asynapsis at diakinesis

with 108 chromosomes. From observations on squash preparations they described how these asynaptic mother cells divided by an abbreviated meiosis to produce diads; a division process in fact almost identical to that in apogamous A. aethiopicum. Spore counts from sporangia showed 28 - 30 apparently good spores in each, but these authors were unable to record anything regarding germination. The chromosome number compared with that of the morphologically similar Trichomanes insigne v.d.B forma α possessing normal meiosis with 36 chromosome pairs led them to suggest that forma β was an asynaptic triploid. The possibility that it was also apogamous was not considered.

Bell (1960) working on Trichomanes proliferum Bl. from Gunong Poe, Sarawak saw an asynaptic diakinesis with 108 univalents. Again the sporangia contained 32 apparently well-filled spores. Because of the small amount of material available no further division stages were seen but it seemed likely that meiosis would have been similar to that in Trichomanes insigne v.d.B forma β.

Since the cytological behaviour of these two species of Trichomanes would lead to an unreduced chromosome complement in the spores, Bell suggested that they could be apogamous; a mode of reproduction which would be necessary if their chromosome number were to remain stable. The evidence is therefore strongly indicative of cytological behaviour similar to that accompanying apogamy in the A. aethiopicum complex being present in the Hymenophyllaceae.

An explanation for the origin of apomixis has provided a challenge to botanists for a considerable time, Apomicts are frequently present together with sexual species in complexes or groups where both polyploidy and hybridisation occur and Gustafsson (1947) after reviewing the

evidence in relation to polyploidy and apomixis, chiefly in the flowering plants, concluded that "hybrid structure facilitates but does not cause apomixis". (p. 137).

There is also a good deal of indirect evidence for a hybrid origin in many examples of apogamous ferns of the more usual type (Manton, 1950; 1961), although no case of apogamy has been synthesised artificially between two sexual individuals. Much of this evidence is derived from the irregular pairing observed at meiosis in the 16-celled sporangia; however owing to the peculiar manifestations of apogamy in the A. aethiopicum complex (i.e. complete asynapsis at meiosis) no similar evidence on their origin is available from this source.

The lowest level of ploidy so far known amongst the apogamous plants in the complex is the octoploid level. Nothing is known yet regarding the ploidy or even existence of apomicts in this complex on other continents but the widely distributed nature and frequency of apogamous octoploids in Africa suggests that apogamy has arisen at this level of ploidy. Further, the morphology and distribution of the octoploid apomicts, particularly in southern Africa, show certain features which substantiate the possibility of a hybrid origin.

The octoploid apogamous plants on the whole possess a denser ramentum of scales and are more coriaceous and in many cases less dissected than the sexual octoploids (see scatter diagrams, figs, 6 and 7). In these features they frequently resemble the sexual dodecaploids more closely. In addition the frond shape and pinnae cutting of representatives of the Rhodesian apomicts (Group II, fig. 82) resemble those of the suspected tetraploid from the Vumba Mountains, Southern Rhodesia (fig. 19):

a striking resemblance since a markedly deltoid frond is not encountered often in the larger representatives of the complex. This may indicate that some of the apomicts have arisen from an octoploid produced by crossing a sexual tetraploid with a dodecaploid.

It is also interesting from a study of distribution patterns in southern Africa that the apogamous plants again appear to be more closely associated with the sexual tetraploids and dodecaploids than with the sexual octoploids. The respective distributions of the apogamous and sexual dodecaploid plants overlap considerably (fig. 87), both bearing a closer resemblance to one another than to those of the sexual tetraploids and octoploids. The significance of this observation however is not clear since the apogamous plants could be ecologically closer to the dodecaploids than say the sexual octoploids by virtue of their mode of reproduction alone. Clearly the apomictic mode of reproduction must possess some advantage over the corresponding sexual ploidy in colonising drier areas. Perhaps a more significant observation from distribution patterns is that the southernmost limit of the apogamous forms in South Africa approximates to that of the tetraploid and dodecaploid sexual cytotypes which are confined to the summer rainfall area, while the octoploids continue westwards into the Cape mediterranean region. There seems here to be a much closer connection between the apomicts and the sexual tetraploids and 12ploids than between the apomicts and the sexual octoploids.

The two apogamous plants from South Africa designated as decaploid must have arisen directly by hybridisation in view of the absence of any sexual plants at this level of ploidy. Whether they arose de novo as

a result of the hybridisation of a sexual octoploid and dodecaploid cytotype, or in fact arose through an apogamous octoploid crossing with a sexual tetraploid is uncertain. Nothing is known yet regarding the inheritance of apogamy in the complex as it has so far proved impossible to synthesise hybrids between the apomicts and sexual plants (see pages 9 and 84). However the 'partial dominance' of apogamy demonstrated in other ferns (Manton, 1950; Walker, 1958) indicates that it would be possible for these decaploids to have arisen in a hybrid combination involving a sexual tetraploid and an apogamous octoploid.

It is clear that the complete asynapsis so characteristic of the apogamous forms of A. aethiopicum is an important prerequisite for their eventual stabilisation in nature. Complete asynapsis however is unknown in hybrids both wild and artificially synthesised, which have been studied among various sexual members of the complex. Such hybrids are often sterile having the usual meiotic disturbances caused by irregular pairing, but pairing is never wholly absent no matter how many univalents may be present. This fact makes it somewhat improbable that the univalents in the apogamous specimens are unpaired solely on account of lack of homologous partners. It seems far more likely that pairing is being prevented by genetical factors actively suppressing the effects of chromosome homology. Genetically imposed asynapsis of this type could have arisen either directly by mutation or by combination of genes through hybridisation so that these facts do not necessarily exclude a hybrid origin of the apomicts.

The nature of other factors involved in establishment of the apogamous life cycle are almost wholly obscure. On the one hand there

is the apparently obligate sequence of diplospores and apogamously reproducing prothalli about which this study has provided no new causal evidence. On the other hand there is the problem of the addition of a restitution nucleus to a developmental sequence normally without such a stage. The A. aethiopicum condition is perhaps the easier one in which to bring this about given the prerequisite condition of total asynapsis, since prolonged delay on the equator of chromosomes unable to move to the poles is often followed by reversion to the so-called resting condition, even when produced artificially as with colchicine treatment. The relative scarcity of the A.aethiopicum type of sporangial development among apogamous ferns in general may therefore perhaps be attributed more to the infrequency of genetically imposed asynapsis than to any intrinsic peculiarity of the processes described in chapter VI.

Summarising the foregoing it would appear that the octoploid level of ploidy in the complex is particularly favourable for assembling the necessary factors for producing the apomicts and that these factors could have been brought together through hybridisation.

The apogamous members of the A. aethiopicum complex in Africa show a considerable range of frond morphology at the octoploid level as shown by the morphological and geographical groups in Chapter VI (p. 94 et seq.). This polymorphy can only be feasibly interpreted on the basis of a separate origin for each of the different morphological types e.g. A. filare (Forsk) Alston (Group I) or A. aethiopicum, Rhodesias (Group II). It may therefore also be concluded with some confidence and regardless of their mode of origin that apogamous plants

have arisen more than once during the evolutionary history of the complex.

Discussion of cytology of the hybrids between the sexual forms of the A. aethiopicum complex.

Parallel evolution of more than one kind undoubtedly also affects the sexual members of the group. Both cytological and morphological criteria reveal a confused and complex situation. On the one hand there is evidence for cytological autopolyploidy but on the other also evidence for genetical and morphological diversity.

As has already been mentioned in regard to the hexaploid hybrids (p. 74) little precise information on the mutual relations of tetraploids and octoploids can normally be obtained from cytology alone since pairing in these hybrids is too uniform. Nevertheless these hybrids do throw light on the nature of the octoploids in a general way and combined with results from other hybrids, on the cytological composition of the complex as a whole.

The analyses of chromosome pairing in the hexaploid hybrids, both wild and artificially synthesised, approximates in most cases to 72 pairs or associations and 72 or less univalents. This probably means that the tetraploids are closely related to the octoploids and are able to pair their chromosomes with partners present in the octoploids, but it should be noted this has not been proved. The octoploids, however, are not true allopolyploids in the classic sense e.g. Raphanobrassica as considerably less than 72 univalents have been observed in many hexaploid hybrids, which in the presence of approximately 72 paired groups or associations indicates some multivalent formation. Multivalents have also been certainly identified in many hybrids but as mentioned on pages 61 and 62 it has generally only been possible to infer their approximate numbers

from chromosome totals. Such indications of multivalent formation have been seen in one wild hexaploid hybrid (p. 89; involving the octoploid B.485, Kericho, Kenya) and in the artificial hexaploid hybrids (summary p. 73) involving four further octoploids (8x Kenya; Schelpe 4281, S.Africa; B.263, S.Africa; B.379, A. demerkense), which suggests the presence of some autosyndetic capacity in each of these five octoploids.

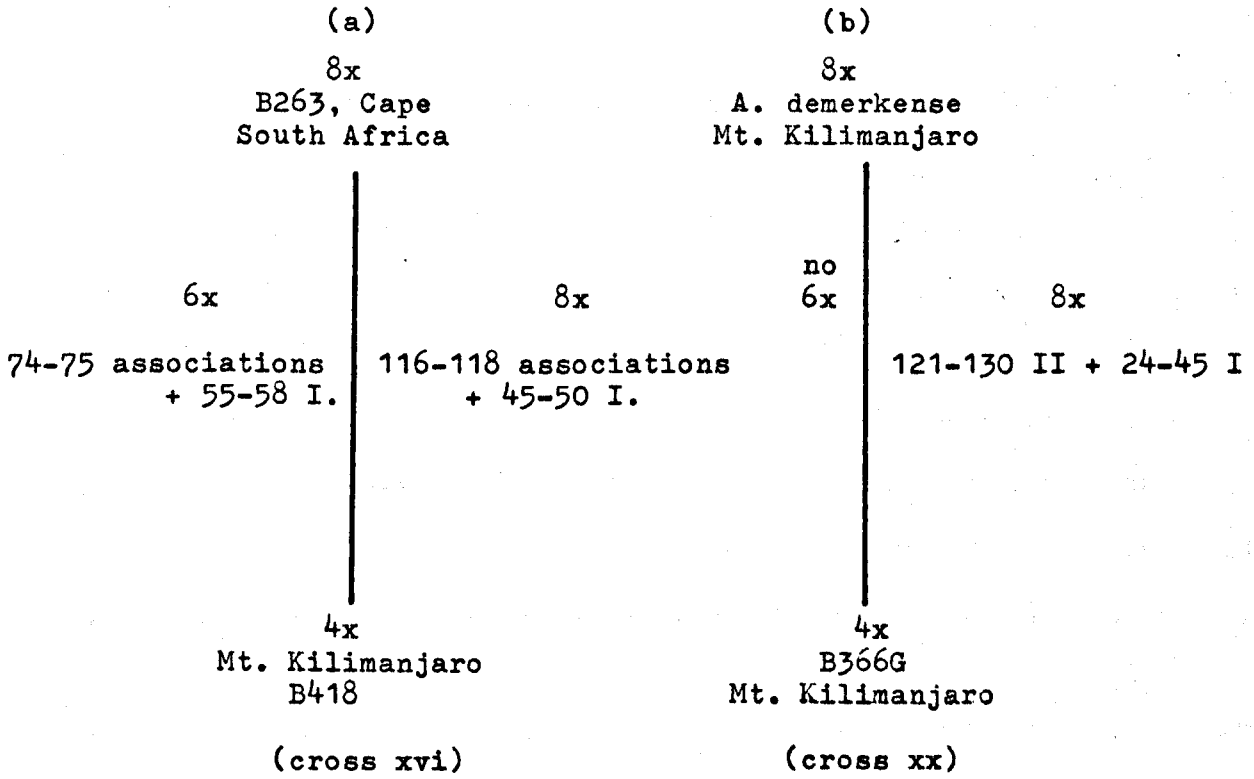
Clearer evidence for autosyndesis in two of the octoploids has been obtained from the cases where, during the synthesis of hexaploid hybrids, functioning of unreduced gametes from tetraploids led to the formation of octoploid hybrids.

In the first case (cross xvi, p. 70-71) and quoted on page 74 both a hexaploid and octoploid hybrid were obtained from the same tetraploid and octoploid parents. The analyses of chromosome pairing at meiosis for these hybrids are reproduced below (a). Since the octoploid can only have arisen by an unreduced gamete from the tetraploid it follows that 72 pairs of the 118-122 associations encountered must have been contributed by this gamete. The remaining 46-50 pairs must therefore have arisen by autosyndetic pairing among chromosomes derived from the octoploid.

From this information it might be expected that, when an unreduced gamete is not involved, the normal hexaploid hybrid of the same parentage would have either 46-50 autosyndetic pairs with the remaining chromosomes univalent or alternatively that 46-50 trivalents among a total of 72 associations would be encountered if allosyndesis as well as autosyndesis can occur. In the latter case only 22-26 univalents would remain.

The actual pairing encountered in the hexaploid hybrid as indicated on the left of the diagram (a) corresponds to neither of the two expected

possibilities but the presence of more than 46-50 pairs indicates some allosyndesis is occurring. However the number of univalents is too great and the inferred multivalents too few for complete allosyndesis, as well as autosyndesis to the extent shown by the octoploid hybrid.



Summary of the chromosome pairing observed in the two crosses where functional unreduced gametes gave rise to octoploid instead of hexaploid hybrids.

The presence of approximately 72 associations in the hexaploid suggests that allosyndesis predominates i.e. all the chromosomes contributed by the tetraploid pair with partners from the octoploid and any pairing in excess of 72 bivalents being indicative of the autosyndetic capacity among the chromosomes of the octoploid. It is therefore likely that homologies present between chromosomes in the octoploid are not being fully expressed in the hexaploid hybrid, where autosyndesis can probably

only show in multivalent formation. It is nevertheless important to note that evidence for autosyndetic capacity among chromosomes derived from the octoploid parent is present in both hybrids, although it is much more clearly expressed in the octoploid hybrid where this internal pairing can show in bivalent formation.

The second case of octoploid hybrids, involving the functioning of unreduced gamets, arose during attempts to synthesise hexaploid hybrids between the octoploid A. demerkense and tetraploid A. aethiopicum var. tripinnatum Baker. (B. 366 G) from Mt. Kilimanjaro (cross XX, p. 72). Using similar reasoning as for the first case above, the chromosome analyses from the octoploid hybrids (diagram (b) above, right) would indicate 49-58 bivalents are being formed among the chromosome contributed by A. demerkense. No hexaploid hybrid of the same parentage is available. However a hexaploid hybrid synthesised between A. demerkense and tetraploid A. aethiopicum (B.418) from Mt. Kilimanjaro (cross XIX, p. 71) shows the octoploid to be capable of some autosyndesis but again the phenomena is more clearly expressed in the octoploid hybrid.

Autosyndesis has also been unequivocally demonstrated among dodecaploid members of the complex. On crossing the two dodecaploids from Madeira and South Africa with tetraploids more than 72 bivalents have been observed at meiosis in the octoploid hybrids. The chromosome pairing in excess of 72 bivalents must necessarily be provided in each case by synapsis between chromosomes derived from the dodecaploid parents (see p.78).

On the other hand evidence for some cytogenetic and morphological differentiation within the complex does exist.

The high degree of fertility in hybrids involving only tetraploids

or octoploids of A. aethiopicum contrasts strongly with the sterility of the hybrids involving only the three dodecaploids. The latter show completely aborted spores in the three hybrid combinations studied and in two of these combinations meiosis is known to be irregular (see p.81). Morphologically the three dodecaploids are reasonably distinct from one another (see p.53 et seq.) which in the light of their cytogenetic differentiation probably indicates an independent origin for each of them. Their present allopatric distribution may well indicate that they have been genetically isolated since their origin, thus providing the opportunity for the retention of any divergence their different origins may have bestowed upon them.

At the tetraploid and octoploid levels within A. aethiopicum there is little evidence on criteria of chromosome homologies to suggest any cytological differentiation at either of these levels of ploidy (see pp. 67, 75). Nevertheless some genetic differentiation among the tetraploids might be indicated by the small proportions of aborted spores often encountered in the hybrids between them.

The most distinct example of cytogenetic differentiation within the complex as a whole has been observed at the octoploid level, as shown by the completely sterile hybrids synthesised between octoploid forms of A. aethiopicum and octoploid A. demerkense (pp. 76-77).

In these hybrids meiosis is irregular and they produce only abortive spores although a high degree of chromosome pairing has been observed. An explanation of the chromosome pairing is not possible at this stage since the evidence, mainly from other hybrid combinations, merely indicates that both allosyndesis and autosyndesis are potentially possible in the

hybrids, but is not conclusive as to which if either predominates. In the absence of this information it is not possible to be certain of the nature or extent of the differentiation between A. demerkense and octoploid A. aethiopicum. The fact, however, that the meiotic analyses from two of the hybrids are not outstandingly different from that in the octoploid hybrid (cross xvi, pp. 70-71) which produces morphologically good spores perhaps suggests genetical rather than cytological differentiation.

There is some morphological evidence to suggest that a further high altitude taxon A. goetzii Hier. (see Appendix) may be involved in the origin of A. demerkense. It is therefore virtually certain that the origin of A. demerkense cannot be discussed in terms of A. aethiopicum alone and caution in its interpretation must be exercised until A. goetzii has been more fully investigated, both in relation to A. demerkense and the various cytotypes of A. aethiopicum, particularly the tetraploids.

GENERAL DISCUSSION.

It is evident that much of the cytogenetic information accumulated during this investigation is of a complex nature, often permitting alternative interpretations of the data to be made. Nevertheless it is clear from the evidence for autosyndesis in the sexual forms that the sexual octoploids and dodecaploids are not true allopolyploids according to the categories of Stebbins (1947, 1950), as might have been suggested by their regular bivalent formation. These polyploids combine characteristics of both allopolyploids and autopolyploids and are therefore best referred to as auto-allopolyploids.

The morphological and cytogenetic differentiation which has become evident at the sexual octoploid and dodecaploid levels during the morphological and experimental studies is thought to represent independent origins for A. demerkense and for the three dodecaploid forms of A. aethiopicum. Furthermore it has been concluded that the octoploid apomicts have arisen more than once during the evolutionary history of the group. A common origin for the polyploids at any one level within the complex therefore cannot be presupposed. In this connection it is interesting to speculate whether the morphological variation at both the sexual tetraploid and octoploid levels within A. aethiopicum is also partially the consequence of diverse origins.

The probability of more than one origin for the octoploids is perhaps increased by the demonstration, during the experimental studies, of the formation of octoploid hybrids from a tetraploid and an octoploid, when the former produces an unreduced gamete. In the two crosses where this has been achieved artificially the plants produce considerable quantities

of good spores which in one case have germinated and the prothalli given rise to young sporelings. It is conceivable therefore that stable octoploids could arise in this way in addition to the more conventional doubling from the tetraploid level.

The frequent production of unreduced gametes by the tetraploids has been a remarkable feature of the cytogenetic aspects of the investigation Further, the occasions when they have been detected can only represent a small fraction of the total number formed. There is good evidence to indicate that these gametes also exist in the wild, since spores used in the hybridisation programme were in some instances collected in the wild (e.g. B.366 G, Mt. Kilimanjaro). While similar gametes have been detected occasionally in other ferns e.g. diploid Asplenium obovatum and Phyllitis hemionitis (Emmott, Thesis 1963) their frequency within the A. aethiopicum complex suggest considerable instability at the tetraploid level. This may well be related to the apparent frequency and scale with which higher polyploids have arisen independently.

One of the very conspicuous features of this investigation has been the complete absence of diploids with 36 chromosomes both among the many living representatives of the complex examined from Africa and among other species sometimes confused with A. aethiopicum (see Appendix). Furthermore, the survey of spore sizes of herbarium specimens from Africa does not provide any evidence to suggest that they are present on the continent. The possibility exists that diploids may never have been present in Africa and members of the complex were already at the tetraploid level when the continent was colonised. Little is known regarding the cytology of the complex in other parts of the world but octoploids have been recorded from

Ceylon (Manton & Sledge, 1954) and Jamaica (T. Walker, personal communication) Therefore the tetraploids, widespread in Africa, are the lowest numbered representatives of the group known.

The meiotic analyses from the hybrids, both artificial and wild, studied in this thesis suggest that the basic unit of chromosome pairing always approximates to 72 chromosomes i.e. the lowest level of ploidy known within the complex, rather than to 36 chromosomes, the real monoploid number in the genus Asplenium. This is substantiated by the fact that within Africa, fertility has only been observed in sexual forms at the tetraploid, octoploid and dodecaploid levels i.e. at numerical intervals of 72 in the polyploid series, while hexaploids and decaploids, representing intervals of 36 in the series are invariably sterile. (The decaploid apogamous plants are clearly rather a special case). A basic chromosome unit or genome of 72 within the complex would indicate that, though cited here as a tetraploid, the lowest level of ploidy is in fact behaving as a diploid. The sterility and behaviour of the hexaploids would then be consistent with the behaviour of triploids present in many groups of ferns and flowering plants. There is therefore good evidence for considering the evolution of the complex in terms of a unit of 72 chromosomes.

Whatever their origin, considerable morphological variation is present at the tetraploid level. Good examples of this are the finely dissected tetraploids described under <u>var tripinnatum Baker</u> encountered only on the eastern side of the continent in contrast to the less dissected tetraploids found in West Africa and also in East Africa and Nyasaland. This morphological differentiation is not accompanied by any corresponding cytological differentiation since all these tetraploids so far seem to be

largely infertile and able to pair their chromosomes. Genetical differences or even some diversity of origin, however, is not thereby precluded.

For the higher sexual polyploids (octo and dodecaploid) the evidence suggesting cytological autopolyploidy combined with morphological and genetical diversity need not be repeated since it has already been discussed. The regular bivalent formation and absence of multivalents in these polyploids does not preclude an autopolyploid origin since the units of 72 chromosomes making up the reduced complement of for example an octoploid could have diverged under pressure of natural selection over a long period of time. Alternatively a genetic system could have evolved which inhibits multivalent formation.

The conclusion that genetical inhibition of chromosome pairing must be occurring in the apomicts is perhaps relevant also to the cytological behaviour of the higher sexual polyploids. It may well be that the absence of multivalents in the sexual octo and dodecaploids is a manifestation of part of the same mechanism. It may also be responsible for much of the difficulty in interpreting the chromosome pairing in the hybrids by preventing autosyndesis except in certain combinations. A genetic system inhibiting autosyndesis and hence multivalent formation is known to operate in Wheat (Riley, 1960) and some similar control of chromosome pairing could be operating here.

The formation of higher polyploids within the complex has resulted in some ecological differentiation between the different levels of ploidy. A comparison of the typical habitats of the various sexual cytotypes and apomicts shows an increase in level of ploidy to be associated with increased tolerance to dryness. The tetraploids are confined entirely to

forested areas while at the other extreme the octoploid apomicts and sexual dodecaploids are almost entirely removed from forest, often growing in drier areas towards the interior of the continent as in southern Africa. The sexual octoploids generally show intermediate requirements being often closely associated with forest, but are more frequently epiphytic, and being capable of colonising more open usually drier situations, than the tetraploids. A similar increase of tolerance to dryness correlated with an increase in the level of ploidy has been noted in A. trichomanes L. (Lovis, Thesis 1958). Since among the sexual members of A. aethiopicum the relationship appears to be linear, i.e. the dodecaploids do not possess ecologic characteristics intermediate between tetraploids and octoploids, it seems possible that the increase in chromosome number alone has influenced the ecological requirements of the higher polyploids to some extent. The apomicts in relation to this problem are clearly rather different and can probably occupy drier habitats than the two lower sexual ploidies by virtue of their mode of reproduction alone. This would fit them well for colonising drier areas than the sexual plants of corresponding ploidy.

The combined ecological tolerance of the various members means that the complex has been able to colonise a considerable variety of habitats and is consequently widely distributed in Africa. The present distribution however is largely governed by the basic sub-tropical nature of the complex. Therefore within the tropics, members are rarely found growing below 3,500 feet. In this area the distribution tends to reflect the relief features and consists of populations or groups of populations on the mountainous areas, often considerable distances apart, and separated by

lower tropical areas or dry plateaux or plains. The evidence for Pleistocene climates in Africa suggests that the distribution may have been more extensive in the past and that the present day populations can probably be interpreted as reduction of a formerly more extensive distribution.

The broad outline of events during the Pleistocene era in Europe are well known. The climatic changes which led to the glacial advances in Europe also occurred on a world wide basis (Flint, 1947, 1957). There is some evidence for a lowering of the snowline and increased glaciation in the past on many of the tropical mountains in East Africa (Nilsson, 1940).

The parts of the world not directly affected by glaciation were subjected to pluvial phases which were probably synchronous with the glacial phases. These were characterised by cooler and wetter conditions (Flint, 1947, 1957).

The Quaternary chronology of a sequence of major pluvial and non-pluvial phases in Africa has been largely worked out from geological, palaeontological and archaeological evidence from East Africa. However evaluation of the evidence (Flint, 1959) led to the conclusion that there exists evidence for one major pluvial, the Upper Pleistocene Gamblian.

More recently botanical evidence has been forthcoming confirming the geological evidence for climatic changes during the Pleistocene in Africa, comparable with those in Europe. Bakker (1962) found a late glacial and post glacial climatic correlation between Africa and Europe, from pollen investigations. Similar studies in N.E. Angola (Bakker and Clark, 1962) confirm the geological evidence for climatic fluctuations

in Africa since the beginning of the last pluvial and provide supplementary evidence for a general correlation between the last pluvial and the Würm glaciation.

The two most recent botanical studies on past climatic changes in Africa both suggest a considerable downshift of vegetation belts during the Upper Pleistocene. Clark and Bakker (1964) from vegetation, stratigraphy and pollen studies at the Kalambo Falls, N. Rhodesia obtained temperature oscillations bearing a remarkable resemblance to those of the Würm glaciation in Europe. These workers also indicate that during the coldest period of the Upper Pleistocene the Kalambo site (c.3900) was occupied by open woodland which now occurs at 5400 - 6300 feet. This would involve a downshift of vegetation belts of 1500 - 2400 feet. Coetzee (1964) from pollen studies of a core of sediments from Sacred Lake, Mt. Kenya provides proof that the time scale of the late glacial and post glacial periods of Europe can be applied in tropical East Africa. At a dated level contemporaneous with the Oldest Dryas of Europe, the vegetation around the lake was similar to that now found above the tree line in the open ericaceous belt. This would involve a downward shift of 1000 - 1100 m. (3300-3600 feet) in this vegation and a probable drop in temperature of about $8^{o}C$ in this high mountain area.

There have therefore been climatic changes in the past in tropical Africa which, as for the Pleistocene in Europe, have had a considerable influence on vegetation. There would seem to be little reason to doubt that during certain phases of the Pleistocene some members of the complex would have occupied many more localities at lower altitudes. The present distribution pattern of the tetraploids and octoploids in particular has

therefore probably been derived by progressive shrinkage of a maximum distribution attained during a pluvial. This would almost certainly have been intensified by the clearance of forest during a long history of human occupation and activity on the continent.

One of the most interesting distribution problems relates to the widely scattered nature of the three dodecaploids. These are known from Madeira, St. Helena and southern Africa (see fig. 53). Each of them is thought to have had an independent origin and the two from the Atlantic Islands immediately present the question as to whether they arose in situ, or migrated there from the mainland thus representing relicts of a formerly more widespread distribution. In Madeira and St. Helena only dodecaploids are known and there is no evidence from herbarium collections suggesting the presence of any other sexual ploidies. This clearly indicates that these dodecaploids have not arisen recently in situ but does not preclude an island origin and the subsequent disappearance of the lower polyploids.

On the other hand the "island dodecaploids" may have been formed elsewhere and reached the islands by chance dispersal presumably from the nearest mainland. The presence on the Cape Verde Islands of a suspected dodecaploid morphologically similar to that on Madeira suggests that this dodecaploid once possessed a more widespread distribution, which may have included part of the continent of Africa. This dodecaploid could therefore have arisen on the continent and reached the islands from the nearest mainland before the Sahara became as hot and dry as it is today. The particular circumstances of the Madeira dodecaploid then might support a relict concept for the nature of the island distributions of the dodecaploids.

If the two dodecaploids on Madeira and St. Helena are relicts then it seems likely that these islands are particularly suitable in enabling these high polyploids to survive, possibly because of their oceanic nature. This might ameliorate climatic changes in such a way as to enable plants to survive which might otherwise be eliminated by these same changes on a continental land mass.

The Madeira and St. Helena dodecaploids have been seen to occupy small islands and to be isolated from the nearest sexual tetraploids and octoploids by considerable distances. In these respects the dodecaploid from southern Africa is quite different since its distribution, though compact, covers a relatively large area and remains in close contact with the lower sexual ploidies and the apomicts. This may well indicate that the southern Africa dodecaploid compared with those from the Atlantic islands is of a relatively more recent origin. Thus some of the most recent evolution of polyploids in what is obviously a very ancient polyploid complex could well have occurred in southern Africa.

It is interesting that in two other investigations involving polyploidy in the genus Asplenium in recent years either auto-allopolyploidy or autopolyploidy has been recorded. Lovis (Thesis 1958) concluded that the tetraploids and hexaploid forms of A. trichomanes L. are auto-allopolyploids while two other tetraploids A. rutamuraria L. and A. septentrionale (L.) Hoffm. are thought to be autopolyploids in a strict sense (Lovis, 1964). In addition Emmott (Thesis 1963) has concluded that the tetraploids in Phyllitis scolopendrium (L) Newman from America and Japan are ancient autotetraploids. In all these polyploids as well as those in the present auto-allopolyploid complex

multivalent formation is usually absent. This could well be an indication of the antiquity of these polyploids since Asplenium is generally regarded as "a very old genus" (Copeland, 1947).

All previous investigations on polyploidy in ferns have revealed only conventional allopolyploidy with the possible exception of Psilotum nudum (Manton, 1950). The results of the investigations on Aspleniums are therefore of considerable importance in demonstrating that, as well as allopolyploidy, successful formation of polyploids can occur in ferns without complete cytological differentiation of the 'building units', as is often the case in the Angiosperms. Such formation of polyploids in Asplenium is clearly responsible for the many taxonomically critical groups within the genus. The morphological and cytological features frequently aiding differentiation of the different levels of ploidy in an allopolyploid complex ~~being~~ are absent or difficult to detect and therefore subdivision must often rely on polyploid markers, which has been the case with the present complex.

Finally it remains to consider the taxonomic implications of the findings presented in this thesis. The most obvious and clear cut feature in this respect is the cytogenetic evidence supporting the retention of A. demerkense Hier. as a specific concept. Excluding A. demerkense, the morphological and cyto-genetic findings within A. aethiopicum are exceedingly complex. The difficulties of a consistent taxonomic treatment using these criteria have in some ways been increased rather than solved by the investigation to date. This is particularly evident both from the different morphological and cytogenetic findings between on the one hand the sexual tetraploids and octoploids and on the other the sexual dodecaploids

and also in view of the discovery of a large agamic section within the complex. It is therefore perhaps premature to make any taxonomic recommendations at this stage, except for the separation of A. demerkense Hier., bearing in mind also that the African representatives studied are only part of a group widely distributed throughout tropical parts of the world.

SUMMARY.

1. Morphological, ecological and cytological studies have been carried out on African representatives of the Asplenium aethiopicum (Burm) Bech. complex.

2. The complex is made up of both sexual and apogamous forms and is highly polyploid. The sexual forms are represented by three cytotypes namely, tetraploids (n = 72), octoploids (n = 144) and dodecaploids (n = 216) while the apomicts are mainly octoploid (2n = 288) with a few decaploids (2n = 360).

3. Morphological studies of live and herbarium material have revealed few useful macro-characters which could be used to separate either the few taxa already described within the complex or to create new ones. However, the three sexual cytotypes and the apomicts possess distinctive spore characteristics and spore measurements can be used with considerable success to classify cytologically undetermined material. By this means, knowledge of the morphological variation and distribution of the various forms has been extended.

4. Hybrids involving all possible combinations of ploidy have been synthesised among sexual forms. The chromosome pairing at meiosis has been studied in these, as well as sterile wild hexaploid hybrids, as a source of information concerning the relationships of the different cytotypes.

5. The findings concerning the inter-relationships of forms within each of the sexual cytotypes are as follows.

   a) The tetraploids show considerable regional morphological differentiation. All the hybrids synthesised between these tetraploids

are able to pair their chromosomes almost completely and they appear to be largely interfertile.

b) The octoploids are morphologically less variable than the tetraploids and do not display any marked regional variation. The hybrids between them show almost completely regular pairing and produce good spores. When these are crossed with a high altitude octoploid A. demerkense Hier, completely sterile hybrids with irregular meiosis are formed. This suggests that A. demerkense may rightly be referred to a separate taxon and it seems virtually certain that its origin cannot be discussed in terms of A. aethiopicum alone.

c) Three dodecaploids are known from Madeira, St. Helena and southern Africa, which are morphologically distinct from one another. Hybrids synthesised between all three dodecaploids are completely sterile and it is believed that each of the 12ploids has had an independant origin.

6. The apogamous members of the complex fall into three morphological-geographical groups corresponding to North-East and West Africa (A. filare, (Forsk.) Alston), Northern and Southern Rhodesia and finally South Africa. The sporangial development and meiosis of the apomicts show a marked departure from those previously known in apogamous ferns and are described. The cytological behaviour and the possible origin of these apomicts is discussed and it is concluded from the variation in their frond morphology that they have arisen more than once during the evolutionary history of the complex.

7. The pairing behaviour of the hybrids and the numerical intervals between fertile sexual members in the polyploid series indicates the

tetraploids are behaving as functional diploids. The sterility in the hexaploids would then be consistent with the behaviour of triploids in other polyploid groups. This suggests the complex has evolved from the tetraploid level and raises the possibility that the continent of Africa was colonised by the complex at the tetraploid level.

8. The frequent detection in artificial hybrids of functional unreduced gametes from tetraploids suggests considerable instability at this level of ploidy. This may well be related to thefrequency and scale with which the higher ploidies have apparently arisen independently.

9. The hybrids have given little information on the precise origin of the higher sexual ploidies but there is evidence for a high degree of autosyndesis suggesting cytological autopolyploidy in representatives of both the octoploid and dodecaploid levels, although the plants normally show regular bivalent formation. It is concluded that these polyploids are auto-allopolyploids.

10. A comparison of the ecology and distribution of the different sexual cytotypes suggests the increase in level of polyploidy is correlated with an increased tolerance to dryness.

11. The present distribution of the complex in Africa is interpreted as reduction from a formerly more extensive distribution in view of the evidence for past climatic changes on the continent during the Pleistocene. The island distributions of the two dodecaploids from Madeira and St. Helena are thought to be relict and it is suggested that the third dodecaploid from southern Africa is of a relatively more recent origin.

12. Apart from recommending the retention of A. demerkense Hier. as a specific concept, no further taxonomic recommendations have been made at this stage since the investigation to date has increased rather than solved the problem of a consistent taxonomic subdivision of the rest of the complex.

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APPENDIX

As stated in the General Introduction a number of species apart from those dealt with in the main body of this thesis have been studied during this investigation. Most of these species have been satisfactorily separated from the A. aethiopicum complex and also examined cytologically when live material has been available. In addition a considerable amount of artificial hybridisation has been carried out among them and in some instances hybrids synthesised with members of the A. aethiopicum complex. Space considerations have not permitted this work to be presented in detail and also much of it is still largely incomplete. It is, however, already clear that many of the species are interrelated cytologically, being members of further small complexes, but little information is available yet on their relationships with the A. aethiopicum complex.

These species are listed below, together with their chromosome numbers principally to show the grades of ploidy present in species surrounding as it were the A. aethiopicum complex in Africa. They are arranged in such a way as to indicate where groups of related species or small complexes occur. The group considered to be most closely related to A. aethiopicum is placed first on the list.

A. goetzii Hier.	Mt. Kilimanjaro.	n = 72	4x
A. Kassneri Hier.	Aberdare Mtns., Kenya.	n = c. 72	4x
A. Uhligii Hier.	Mt. Kilimanjaro.	n = c. 144	8x
A. splendens Kze.	South Africa.	n = 72	4x
A. multiforme Kr.	South Africa.	n = 144	8x
A. sp. (aff. A. multiforme Kr.)	South Africa.	n = 72	4x
A. splendens Kze var angustatum (Sim) C. Chr.	South Africa.	n = 144	8x
	Tanganyika.	n = 144	8x

(This variety is so distrinct from A. splendens Kze that it should be raised to specific rank.)

A. albersii Hier.	Tanganyika.	n = 144	8x
A. linckii Kuhn.	Tanganyika.	n = c. 72	4x
A. ramlowii Hier.	S. Rhodesia.	n = 72	4x
A. sp. (aff ramlowii and splendens.)	S. Africa. (B. 140)	n = c. 144	8x
	S. Rhodesia. (UMT 7)	n = 144	8x

A. blastophorum Hier. (gemmiferous).	S. Africa.	n =	144	8x
	S. Rhodesia.	n =	144	8x
A. sp. (not gemmiferous) (aff. A. blastophorum)	S. Rhodesia. (Mitchell 391, BM, BOL)	n =	72	4x
A. buettneri Hier.	Ghana.	n =	144	8x
A. stuhlmannii Hier.	Brit. Somaliland.	n =	72	4x
	Kenya.	n =	72	4x
A. stuhlmannii Hier.	Nigeria (Hambler 513,BM)	n =	144	8x
A. jaundeense Hier.	Yaounde, Cameroons. (type locality).	n =	72	4x

ACKNOWLEDGEMENTS.

I wish to record my appreciation and gratitude to the Department of Scientific and Industrial Research, The British Council and the University of Leeds for their financial support during this investigation and also for their co-operation, which made possible the visit to Africa from July 1960 until July 1961. A Research Studentship from the D.S.I.R. was held from October 1959 to September 1962 and in connection with the visit to Africa I was the fortunate recipient of a British Council Travel Grant and of further financial support from the University of Leeds.

My thanks are due to Professor W. Isaac who kindly made facilities available for me in the Department of Botany, University of Cape Town, and also to the authorities of the National Botanic Gardens of South Africa at Kirstenbosch for providing space for live material.

It is impossible to mention here all the individuals who either assisted me in Africa or donated plants. I should like however to thank especially Dr. E. A. Schelpe, Curator of the Bolus Herbarium University of Cape Town, for his valuable guidance and help during fieldwork and for his assistance in many other ways too numerous to mention.

I am indebted to the authorities of various herbaria for allowing me access to their collections and for providing study facilities. These include the British Museum (Natural History), the Royal Botanic Gardens at Kew, the Bolus Herbarium Cape Town,

the National Herbarium, Pretoria and the Southern Rhodesia Goverment Herbarium at Salisbury. I also wish to thank the authorities at Kew for receiving the live material despatched to the United Kingdom from Africa.

The maintenance of the large number of live plants in cultivation has been largely in the skilful hands of Mr. P. Lee and his staff of the Botany Department Experimental Gardens, University of Leeds, whose constant attention and help I gratefully acknowledge. I also thank the technical staff of the Botany Department for assistance in the photographic techniques.

Finally I express with pleasure my grateful thanks to Professor Manton for her advice and assistance at all stages of the investigation. Without her support and encouragment the investigation would not have been begun let alone brought to the present conclusion.

ILLUSTRATIONS.

Figures 1 - 87.

Fig. 1. Meiosis showing 72 bivalents in tetraploid A. aethiopicum from Mt. Kilimanjaro. (B418, X1000)

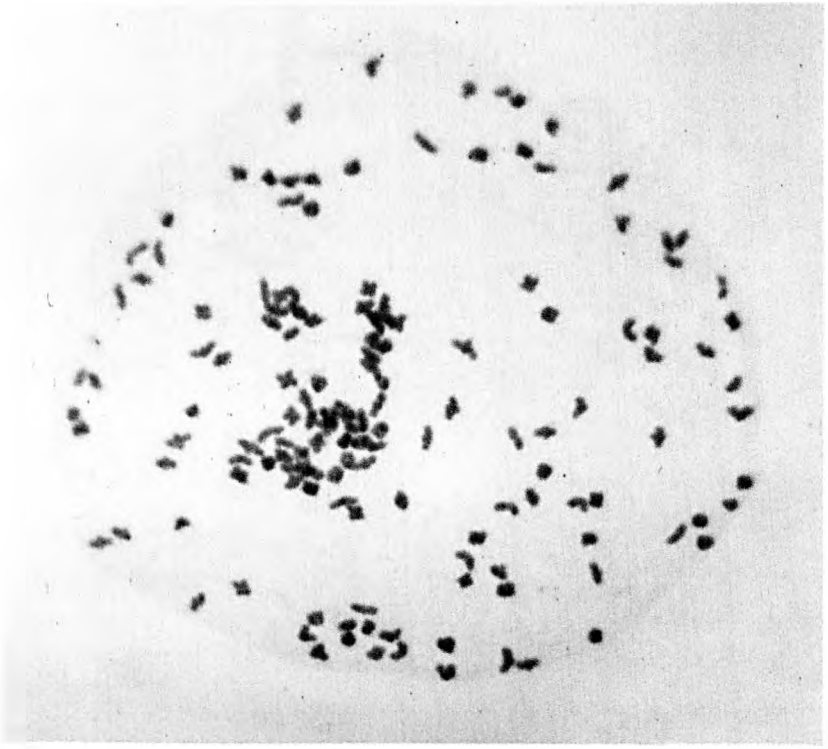


Fig 2. Meiosis showing 144 bivalents in octoploid A. aethiopicum from the Cape Peninsula, S. Africa. (B2, X1000)

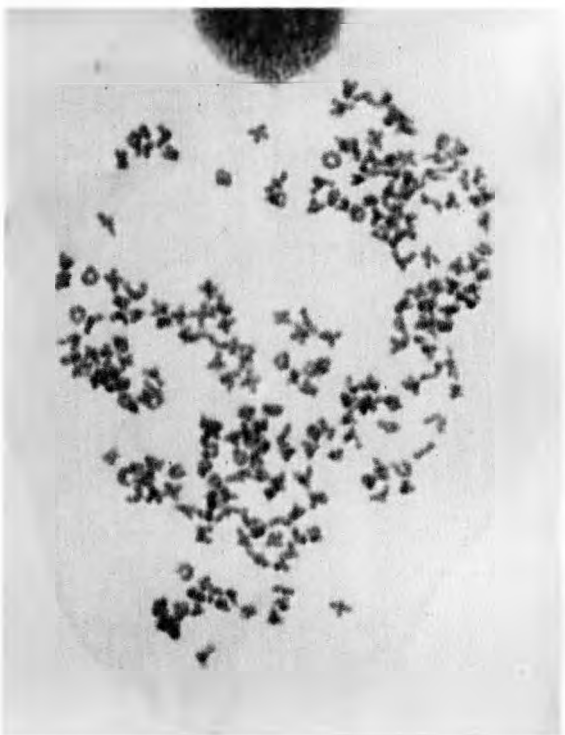


Fig. 3. Meiosis with 216 bivalents in dodecaploid *A. aethiopicum* from St. Helena. (Kerr 137, X1000)

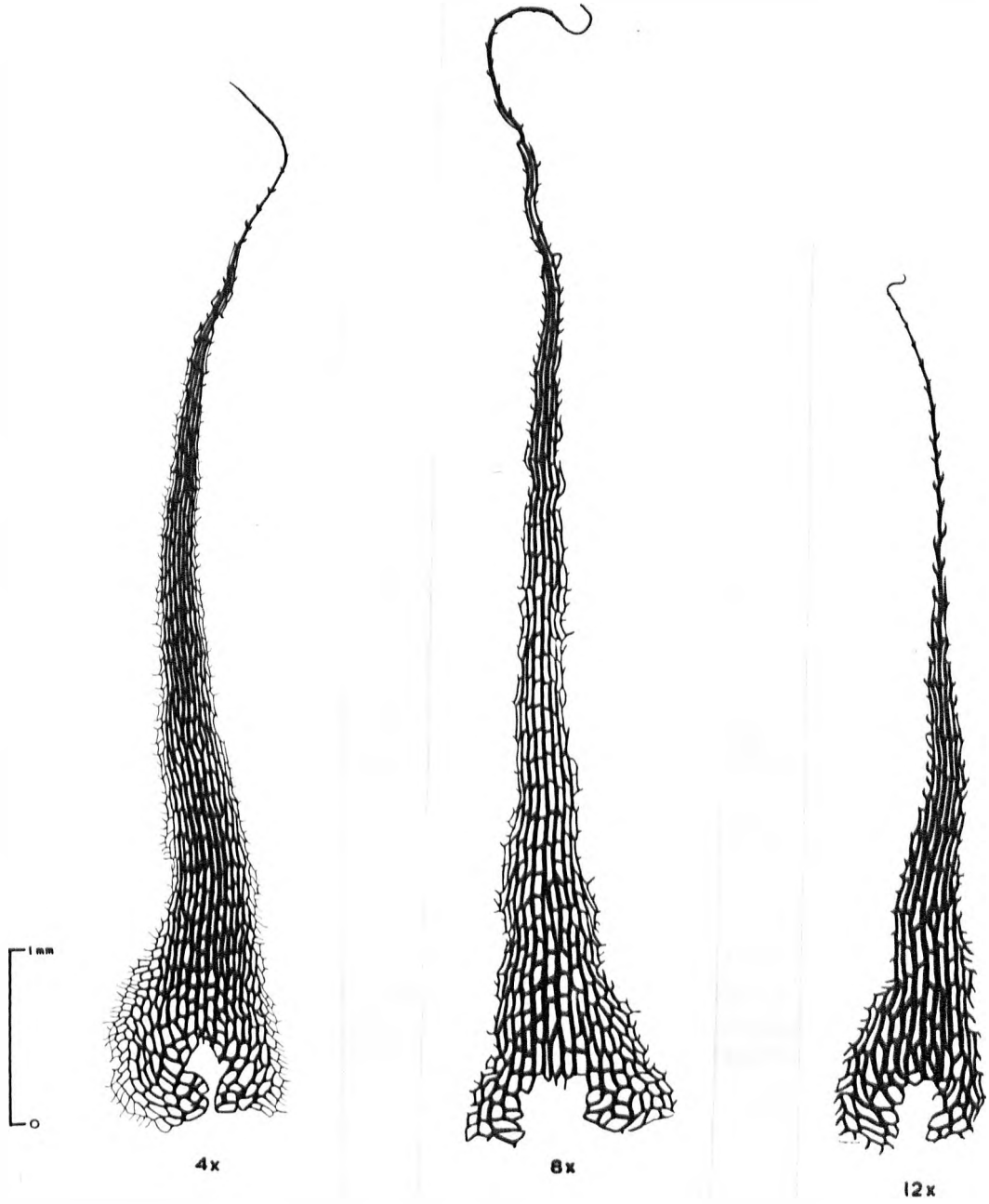


Fig. 4. Rhizome scales from sexual tetraploid, octoploid and dodecaploid A. aethiopicum in South Africa. X25.

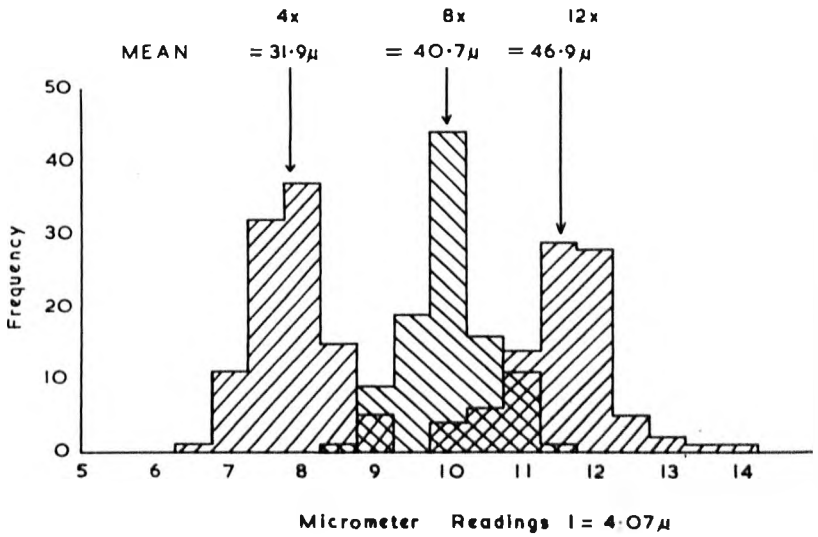


Fig. 5. Histogram of spore length measurements of one hundred spores from each, for a tetraploid, octoploid and a dodecaploid plant from S. Africa.

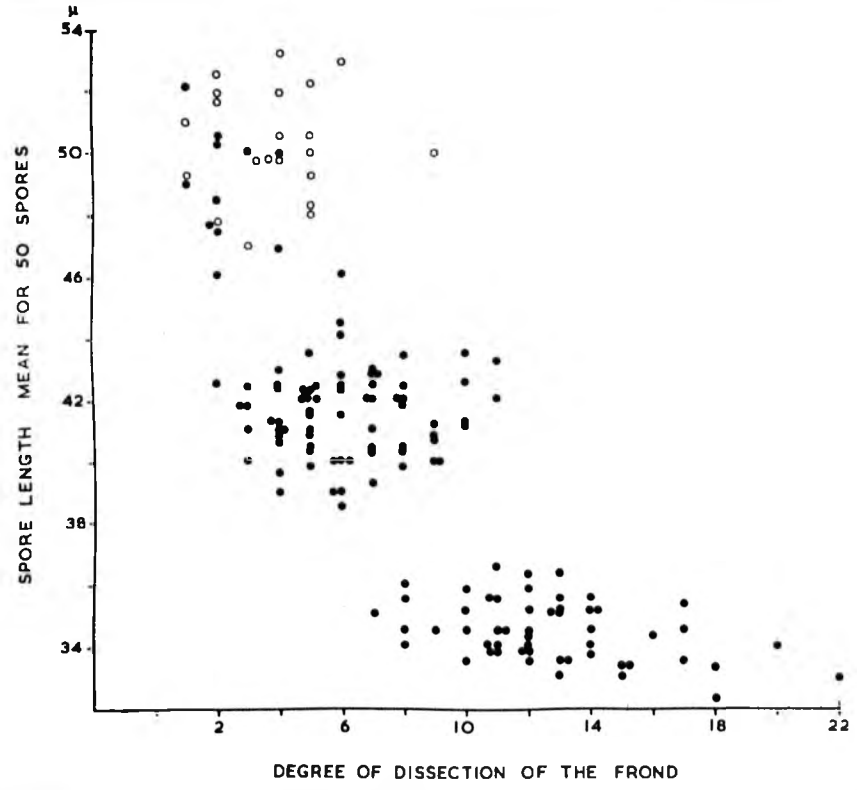


Fig. 6. Scatter diagram recording the incidence of spore length and degree of dissection of the frond (see p. 20, v) of herbarium specimens from South Africa, Each dot denotes one specimen.

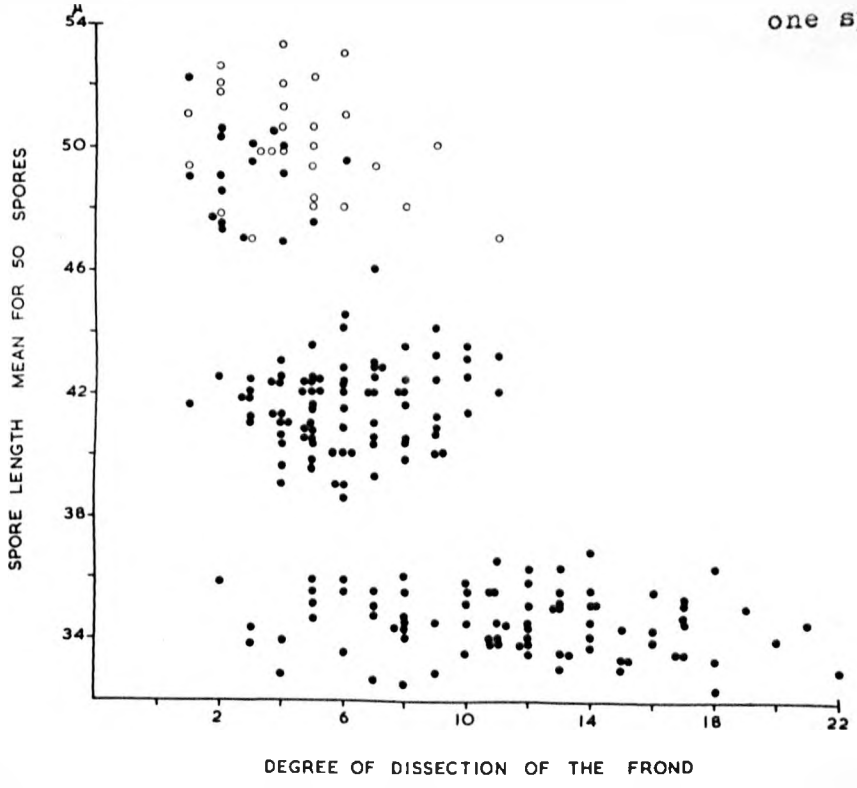
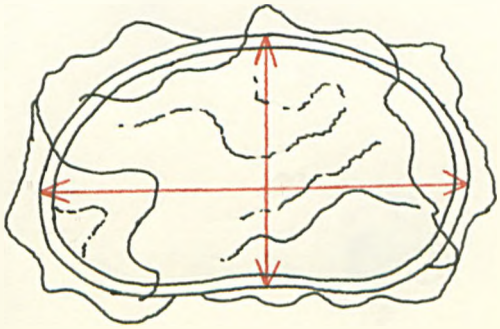


Fig. 7. Scatter diagram, based on that for the herbarium material from S. Africa in fig. 6 above, but also including measurements from herbarium specimens drawn from other parts of Africa where these extend the ranges of the groups appearing in fig. 6.

FIGS. 8 - 13.

Scatter diagrams showing spore length plotted against length-breadth ratio of the spore. Spore length-breadth ratio calculated from the means of spore length and breadth measurements taken as shown in the diagram below. Samples of 100 spores were measured for fig. 8 and 50 spores for figs. 9-13.

Each dot on the diagrams represents one specimen.



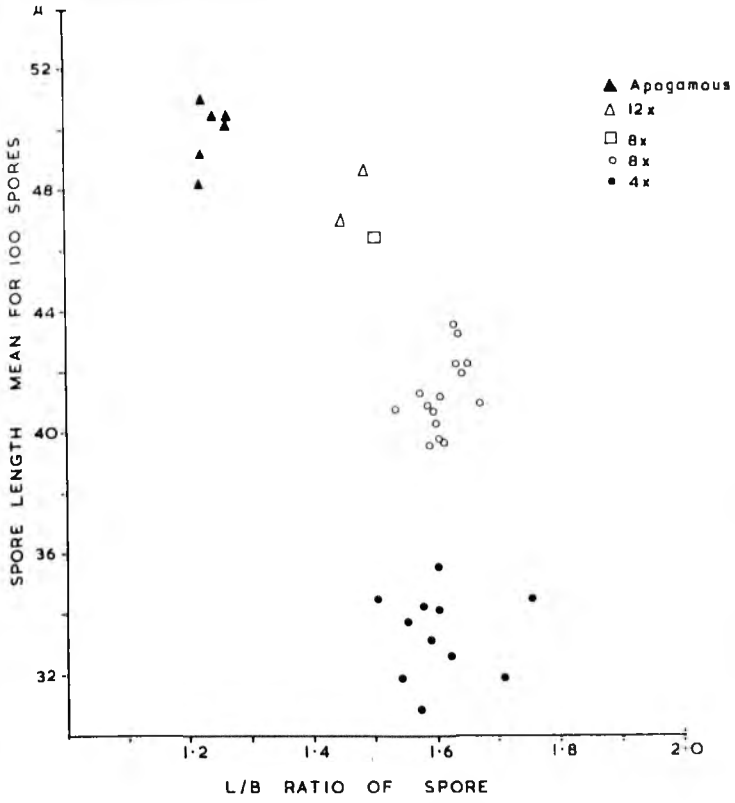


Fig. 8. Scatter diagram for some cytologically authenticated representatives of the complex showing the positions the different cytotypes may be expected to occupy on the diagrams.

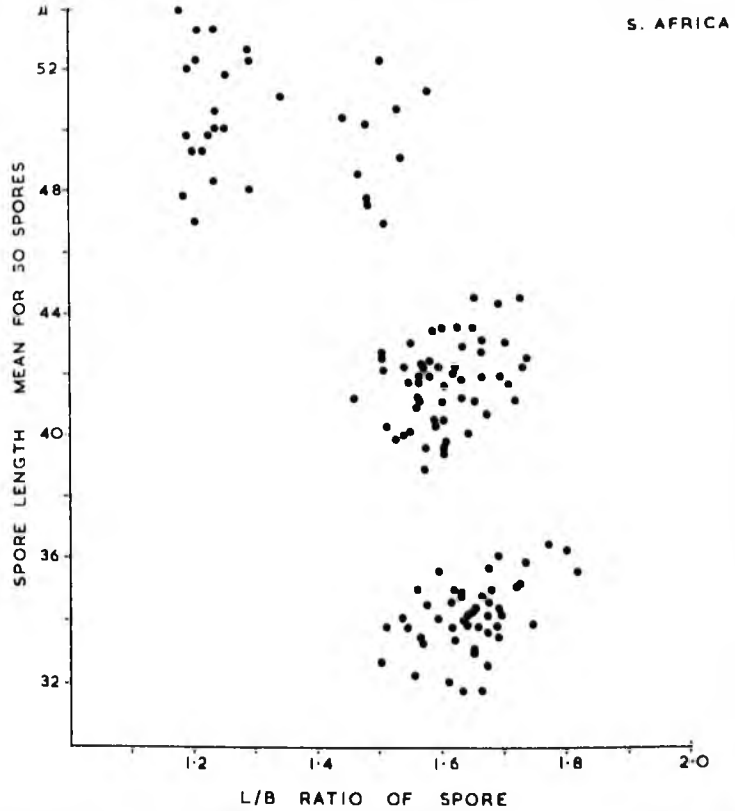


Fig. 9. Scatter diagram for the herbarium material from South Africa.

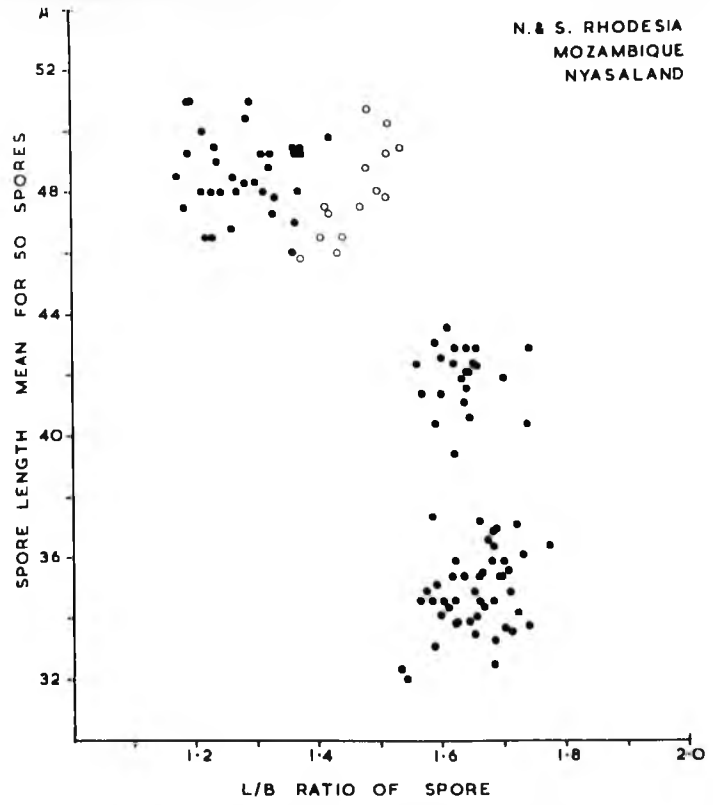


Fig. 10. Scatter diagram compiled from material chiefly from Southern Rhodesia but also includes specimens from Northern Rhodesia, Nyasaland and Mozambique.

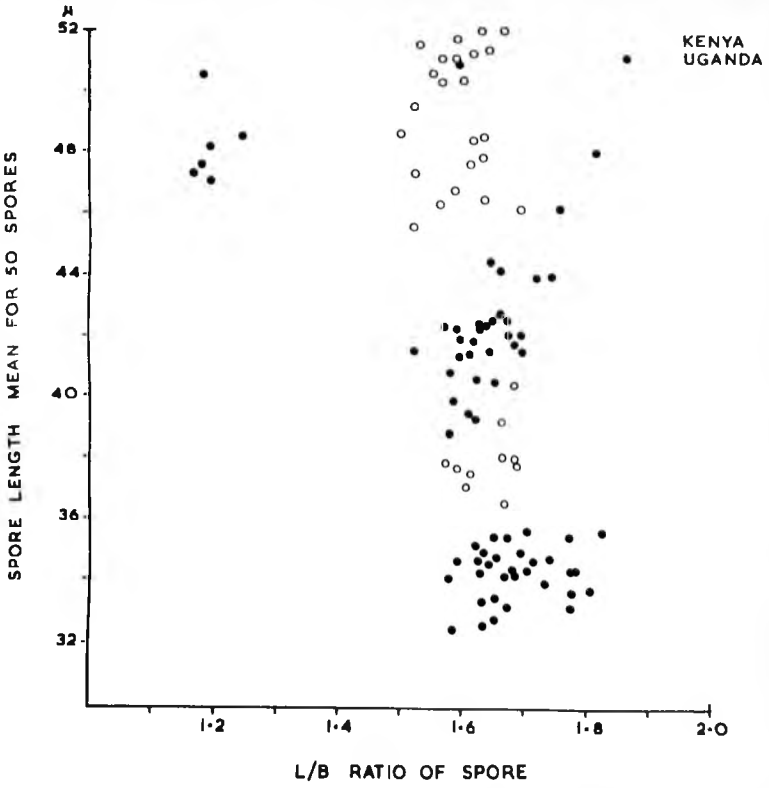


Fig. 11. Scatter diagram for material from East Africa compiled chiefly from herbarium specimens from Kenya and Uganda. Open circles denote the larger spored tetraploid (Aberdare Mtns) and the octoploid (A. demerkense Hier). see p. 23.

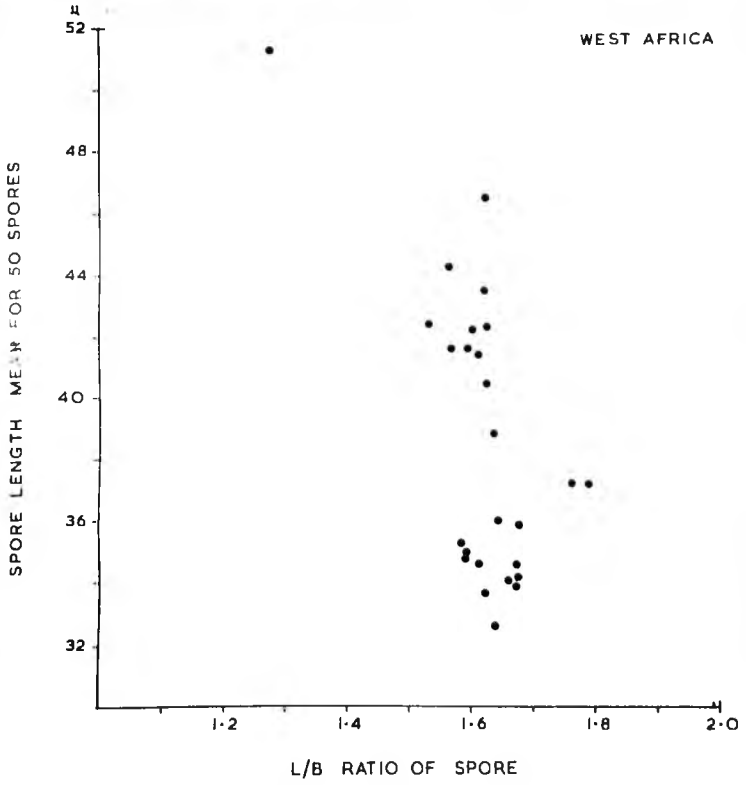


Fig. 12. Scatter diagram for herbarium material from West Africa.

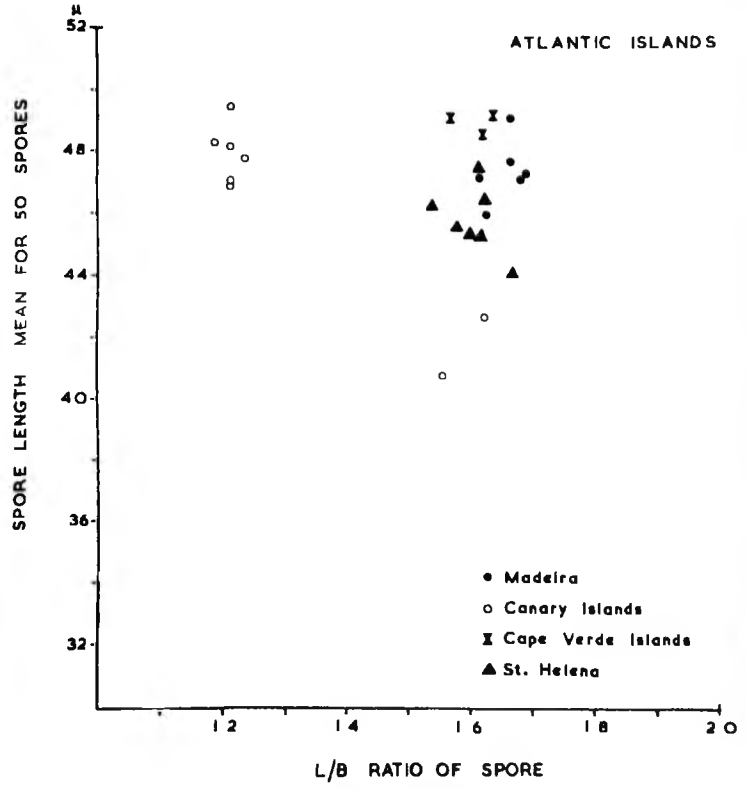


Fig. 13. Scatter diagram for herbarium specimens from the Atlantic Islands - Madeira, Canary Islands, Cape Verde Islands and St. Helena.

TETRAPLOID

FIGS. 14 - 16.

A. aethiopicum (Burm) Bech var tripinnatum Baker

South Africa and Southern Rhodesia.

(OVER)

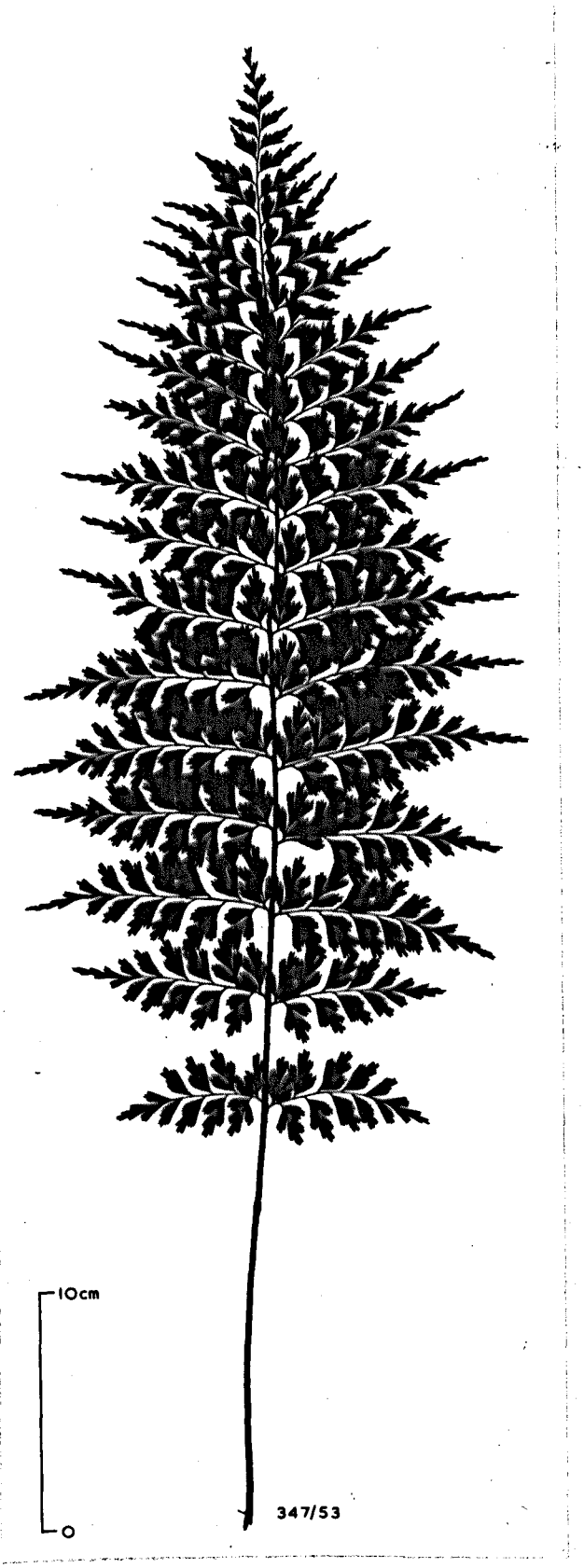


Fig. 14.

A frond from a cultivated plant collected by McNeil from the Transvaal, South Africa. X 1/3.

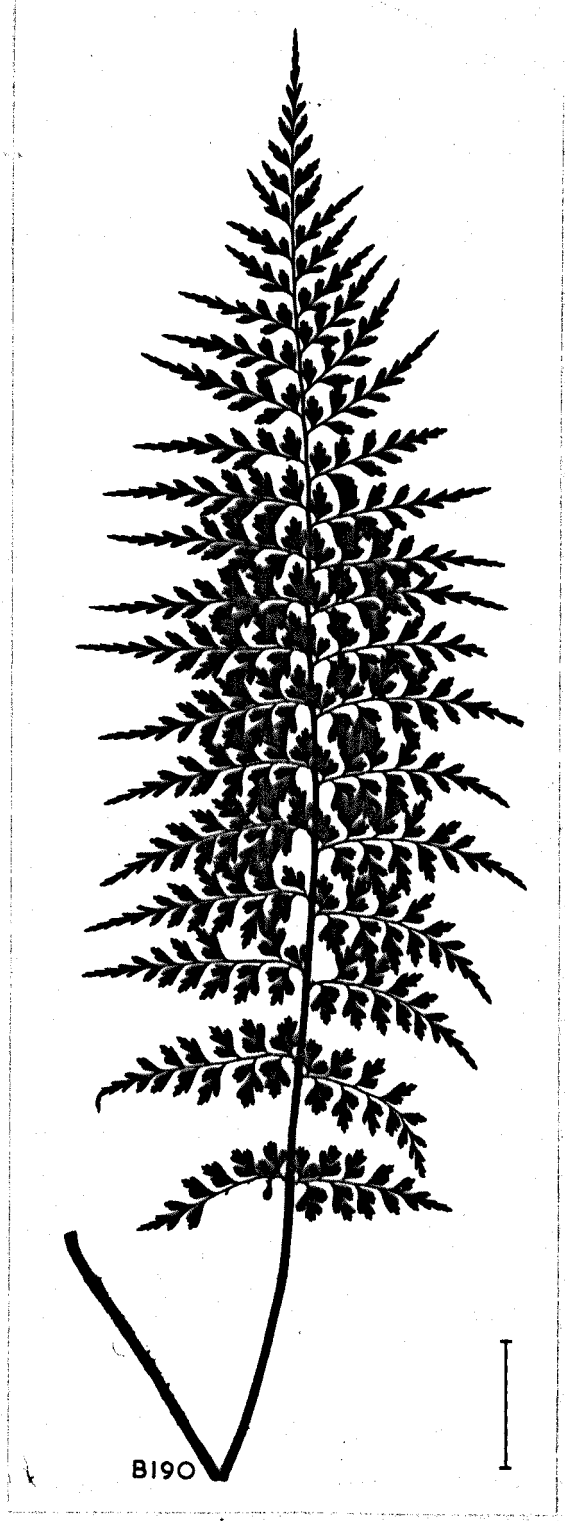


Fig. 15.

Nr. Graskop, Transvaal,
South Africa.
(wild collection)

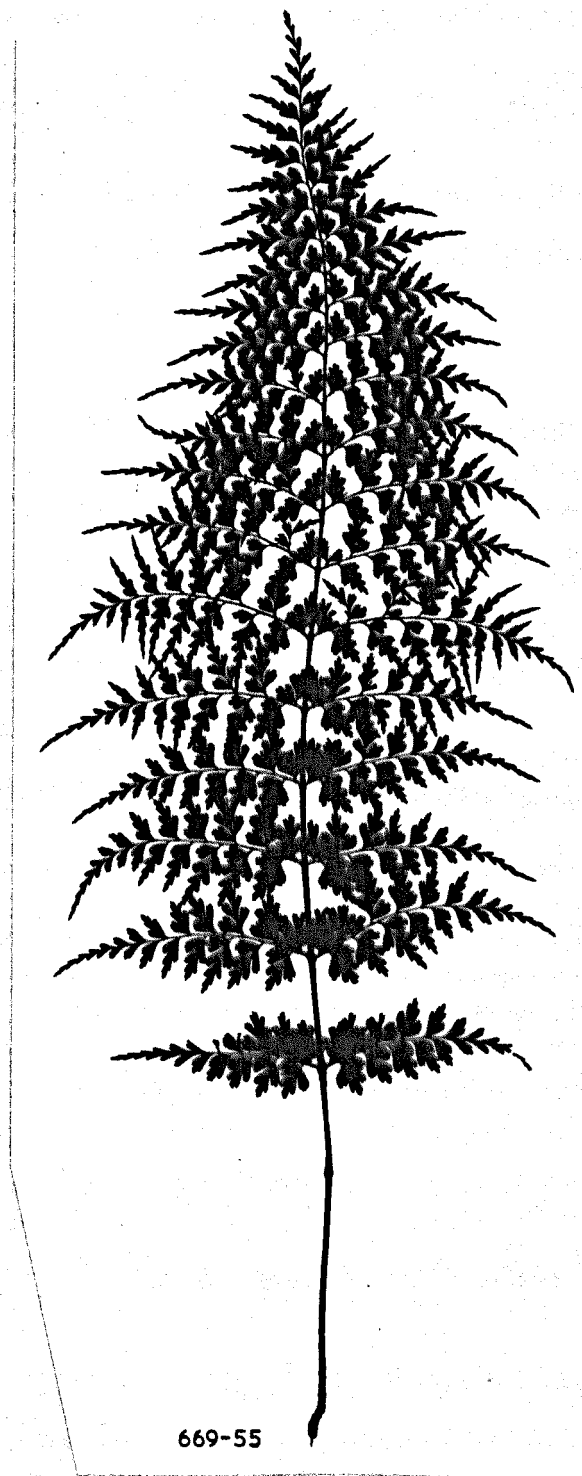


Fig. 16.

Penhalonga Waterfall,
S. Rhodesia-Mozambique border.
(cultivated frond)

Figs. 14-16. "var tripinnatum Baker", S. Africa and S. Rhodesia.
Frond silhouettes. X 1/3.

Fig. 17. A. aethiopicum (Burm) Bech. var tripinnatum Baker growing on a large boulder in the Hogsback Forest, Amatola Mountains, Cape Province, South Africa.

Fig. 18. A. aethiopicum (Burm) Bech. var tripinnatum Baker growing in the open (see p. 28) at The Pinnacle, nr. Graskop, Transvaal, South Africa.

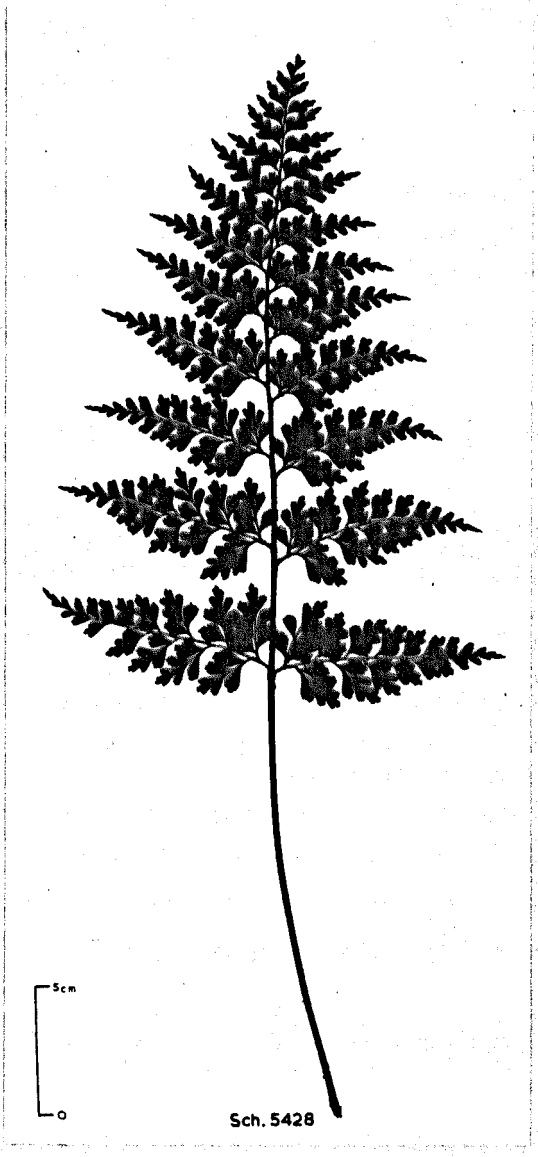


Fig. 19. "var tripinnatum Baker" Vumba Mountains
A silhouette of a frond taken from a cultivated plant (Schelpe 5428) originally collected in the Vumba Mountains, Southern Rhodesia. X 1/3.

TETRAPLOID

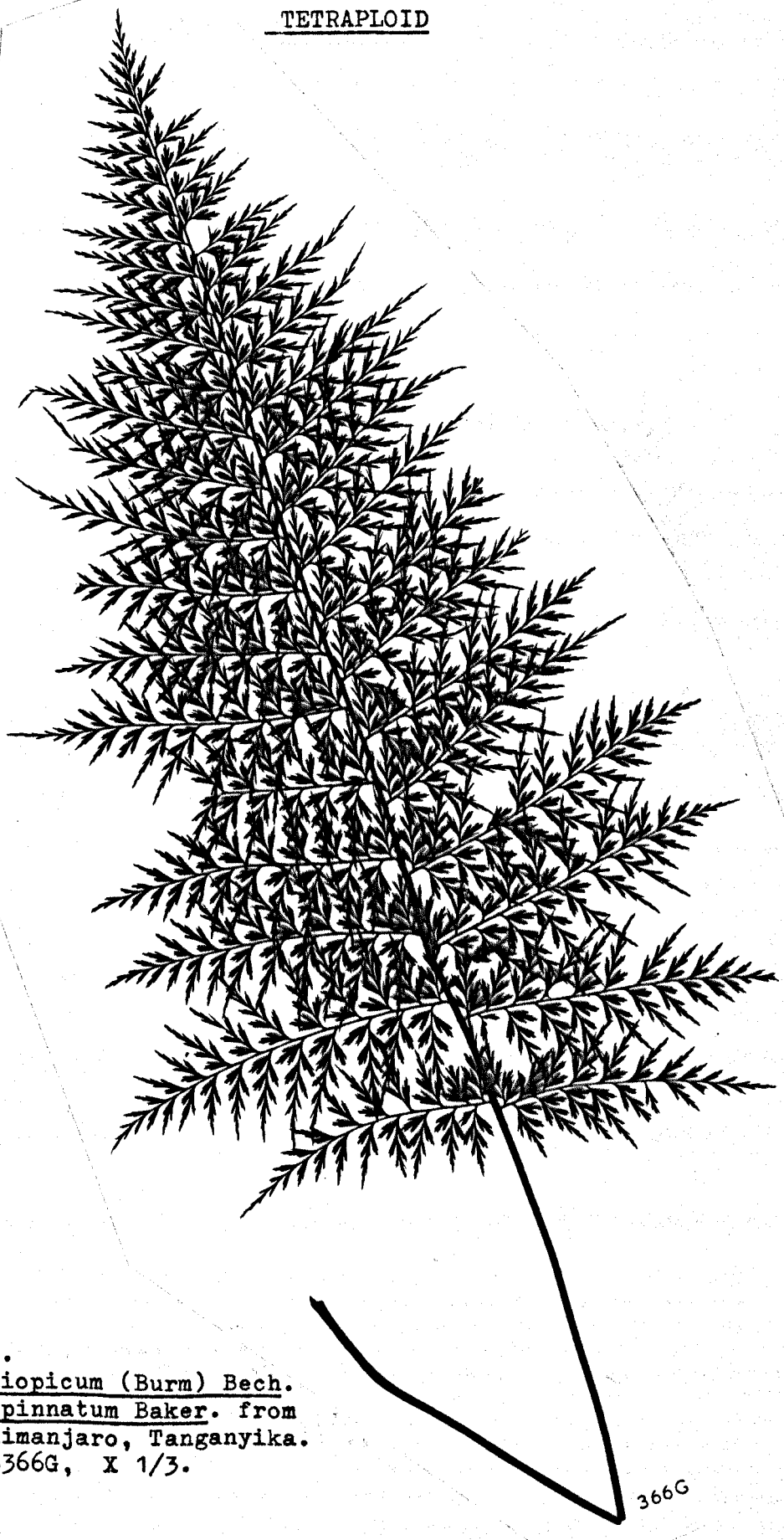


Fig. 20.
A. aethiopicum (Burm) Bech. var tripinnatum Baker. from Mt. Kilimanjaro, Tanganyika.
B366G, X 1/3.

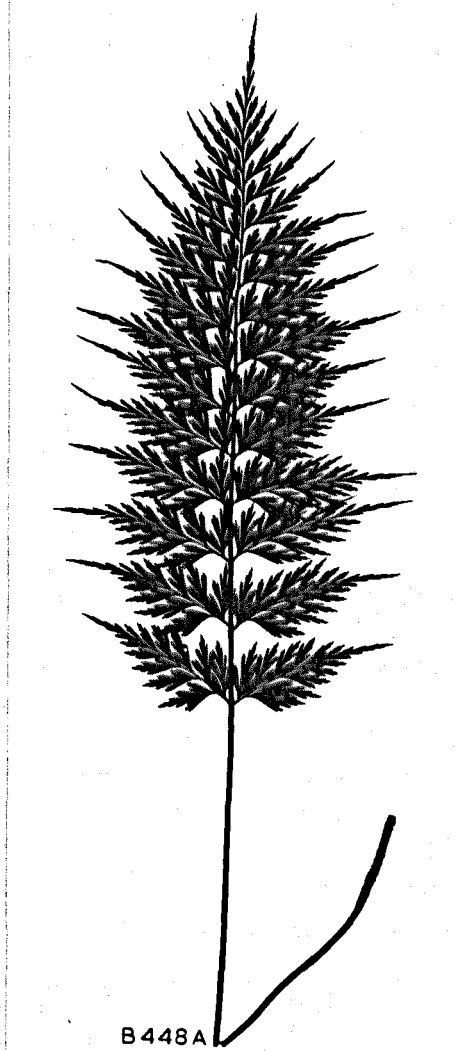


Fig 21.

Fig. 22.

Figs. 21-22. "var tripinnatum Baker" Aberdare Mountains
Silhouettes of fronds collected in the wild from
Nyeri Chania Fall, Aberdare National Park, Kenya.
B448, X 1/3.

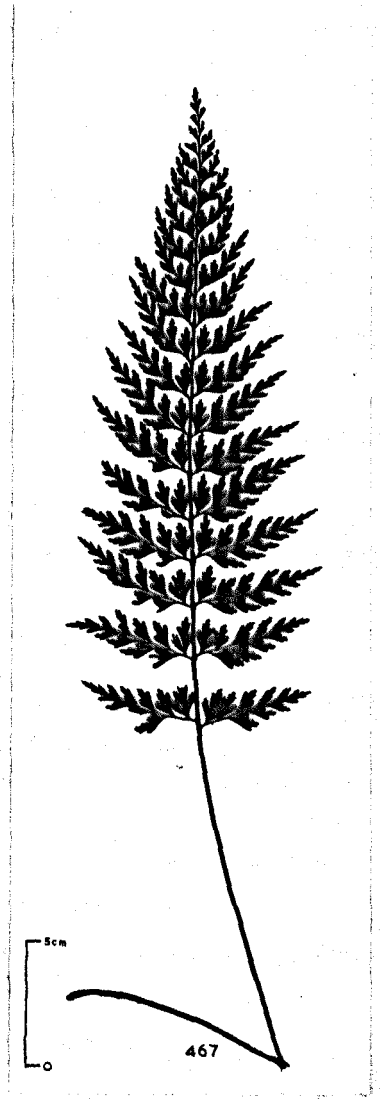


Fig. 23.

"var tripinnatum Baker" Aberdare Mountains.

A frond silhouette of a wild gathering B467 from Queens Cave Waterfall, Aberdare National Park, Kenya. X 1/3.

Fig. 24a. Meiosis in B467 from Queens Cave Waterfall, Aberdare National Park, Kenya. X 1000.

Fig. 24b. Explanatory diagram for fig. 24a (above) showing 76 bivalents and 6 univalents (outlined). X 1500.

TETRAPLOID

Fig. 25. Distribution map for A. aethiopicum var tripinnatum Baker and A. milbraedii Hier. compiled from herbarium records and live material.

'var tripinnatum'
- ● S. Africa & S. Rhodesia.
- ● Mt. Kilimanjaro.
- ◐ A. milbraedii Hier
- ○ Vumba Mtns. & Mt. Mlanje.
- ○ Aberdare Mtns., Kenya.

(compare with less dissected tetraploids fig. 30; octoploids fig. 41; and dodecaploids fig. 53)

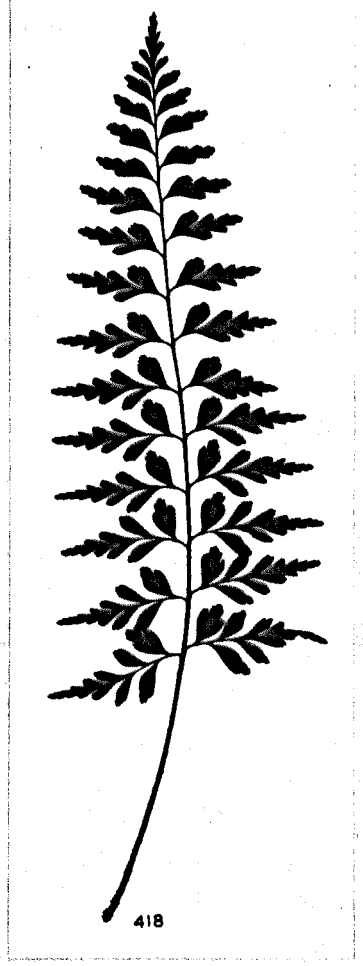


Fig. 26.

B418,
Mt. Kilimanjaro,
Tanganyika.
C. 6000'

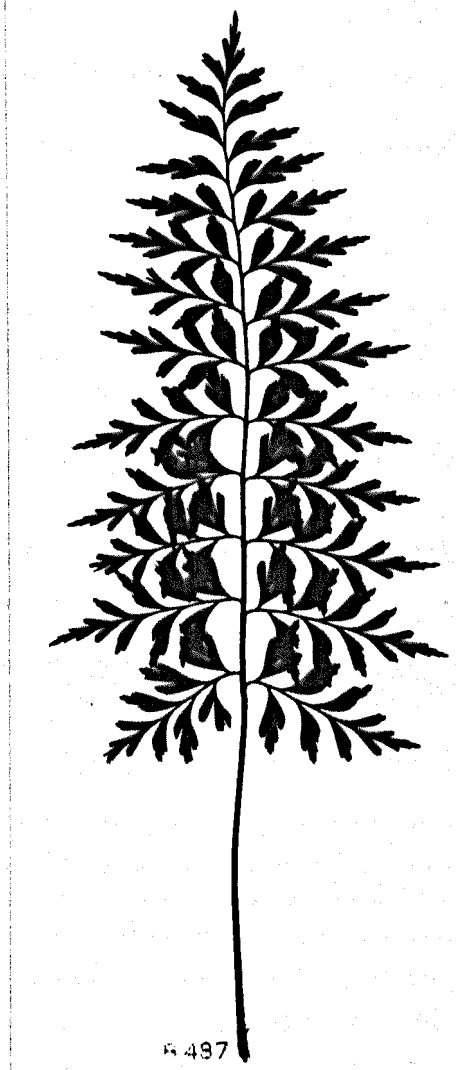


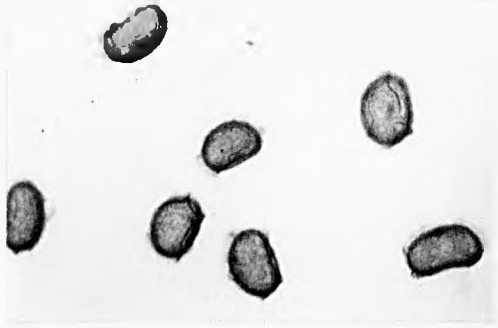
Fig. 27.

B487,
Kericho,
Kenya.
C. 6000'

Silhouettes of fresh fronds from cultivated plants of less pinnate tetraploid forms of A. aethiopicum from East Africa. X 1/3.

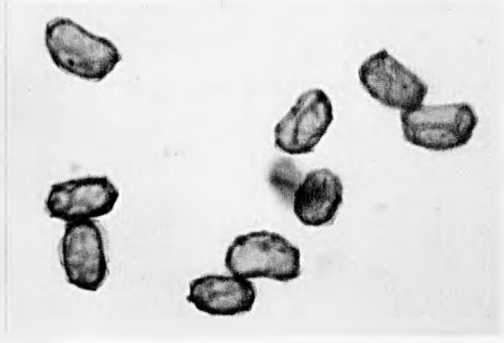
a) var tripinnatum Baker

South Africa.
B157.



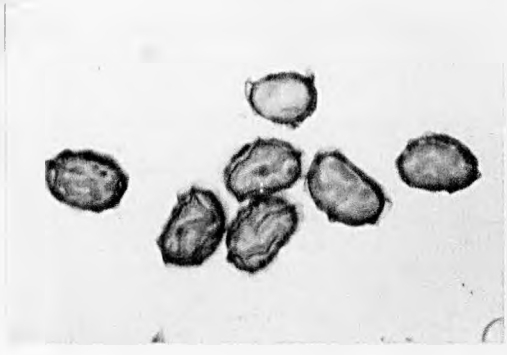
b) var tripinnatum Baker

Kilimanjaro.
B366G.



c) var tripinnatum Baker

Aberdare Mountains.
B448B.



d) Less pinnate tetraploid.

East Africa.
B418.

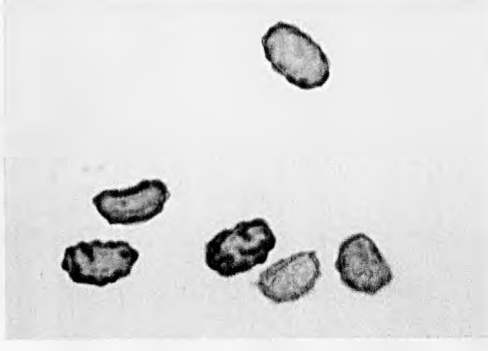


Fig. 28. Spores X 250.

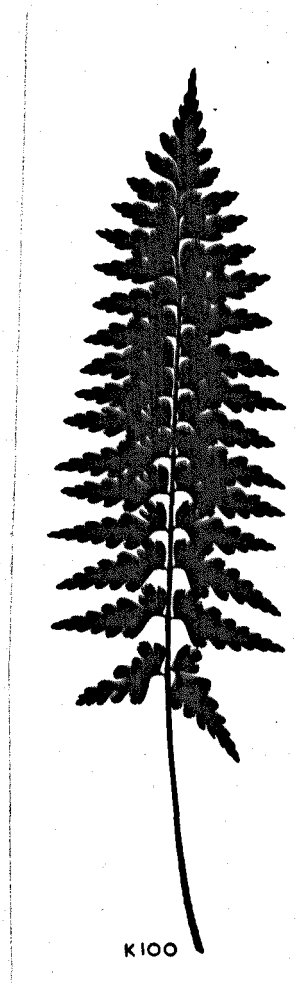


Fig. 29.

Tetraploid A. aethiopicum from West Africa.

A frond from the cultivated plant K100 originally collected from Cameroons Mtn.

X 1/3.

Fig. 30. Map to show the distribution of the less dissected tetraploid forms of A. aethiopicum compiled from herbarium records and live material.

(compare with tetraploid 'var tripinnatum' fig. 25, octoploid fig. 41 and dodecaploid fig. 53)

OCTOPLOID

FIGS. 31-35. A. aethiopicum (Burm) Bech.

8x.

South Africa.

Frond silhouettes. X 1/3.

(OVER)

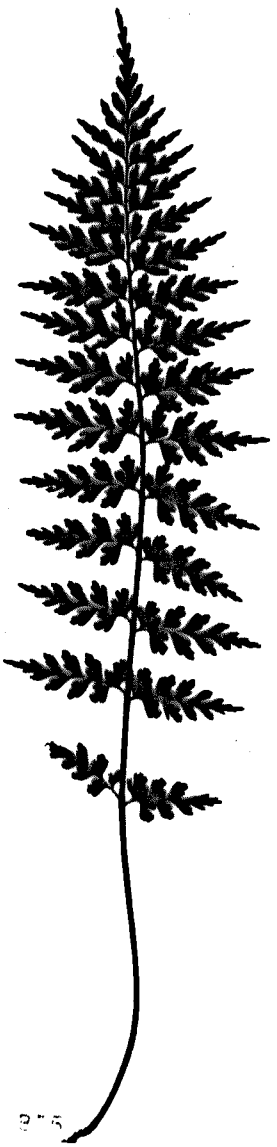


Fig. 31b.

Fig. 31a.

a) B75 & b) B78.
Kalk Bay Mtn., Cape Peninsula.
(wild collections)

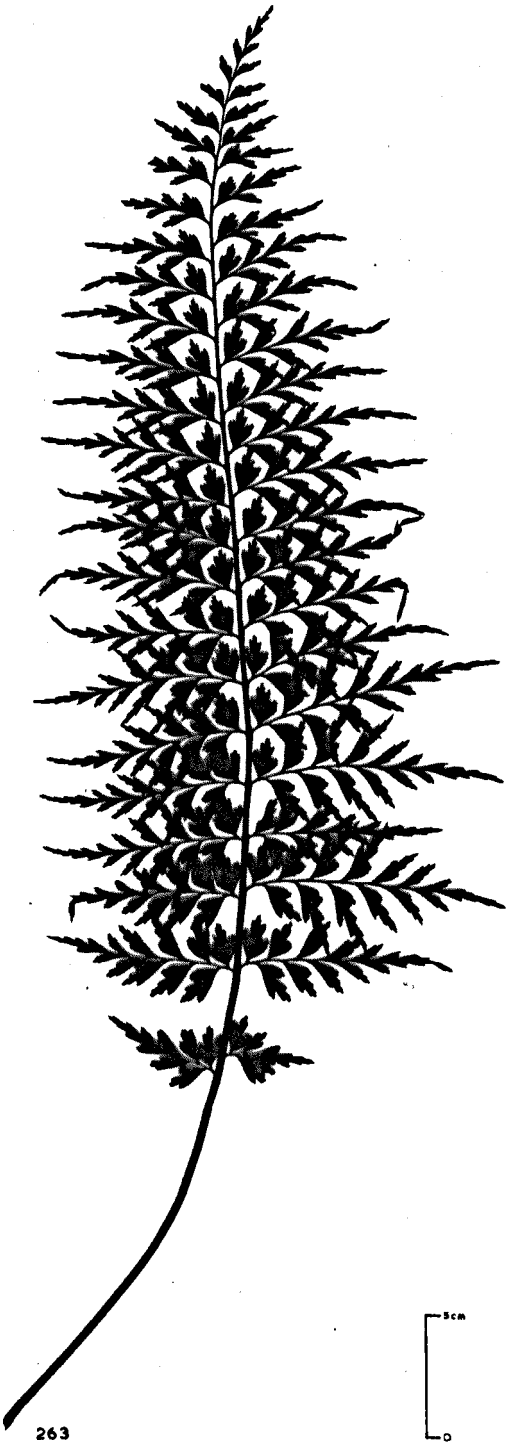


Fig. 32.

B263, Window Gorge, Kirstenbosch, Cape Peninsula.
(cultivated)

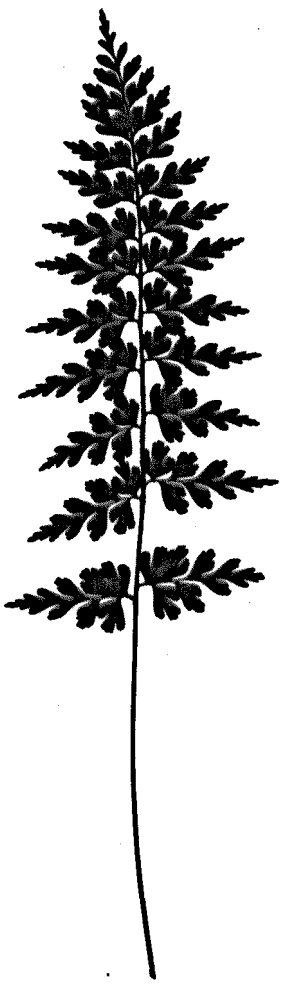


Fig. 33.

B2, Pipe Track, Blinkwater, Cape Peninsula.

(wild)

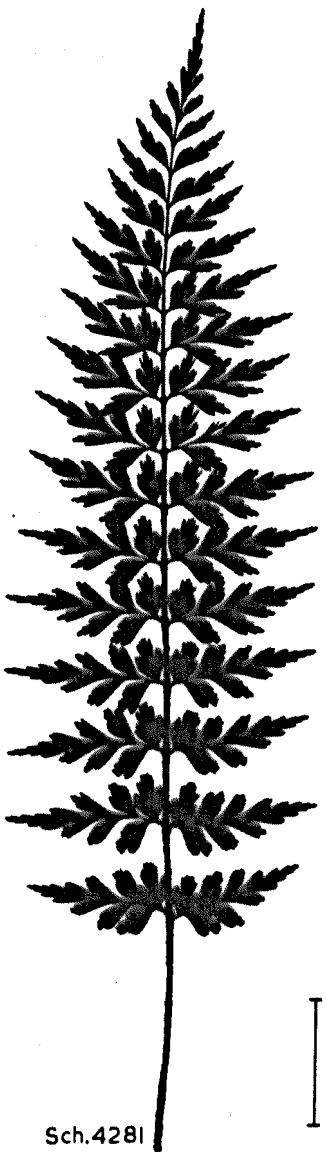


Fig. 34.

Knysna Forest, Knysna, Cape Province.

(cultivated)

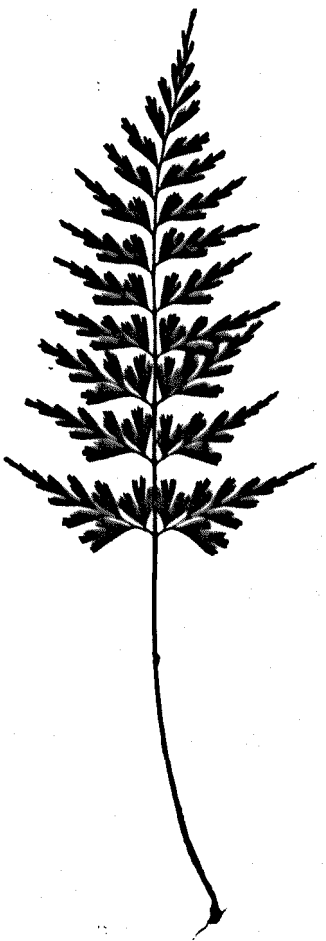


Fig. 35.

B254A, Woodbush, Transvaal. epiphytic.

(wild)

OCTOPLOID

FIGS.36-39. A. aethiopicum (Burm) Bech.

8x.

East and West Africa.

Frond silhouettes. X 1/3.

(OVER)

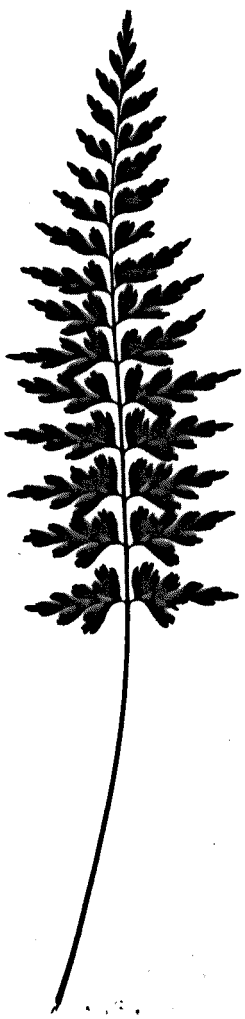


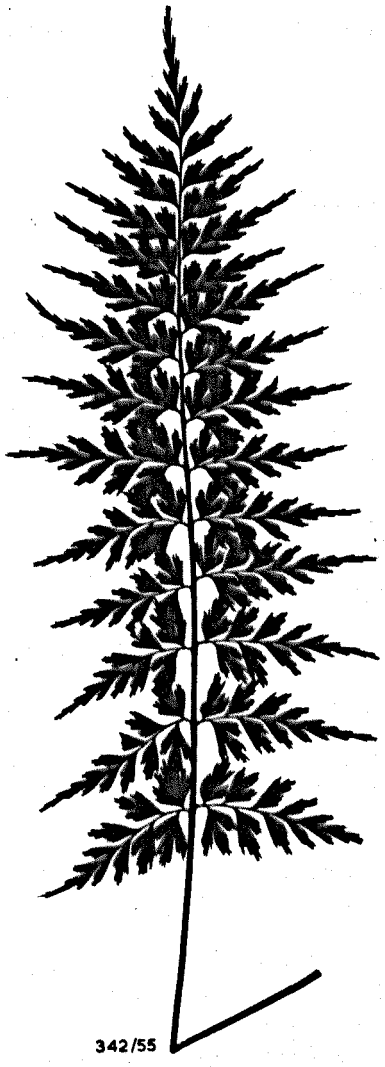
Fig. 36.

B484, Kericho, Kenya.
(epiphytic)

Fig. 37.

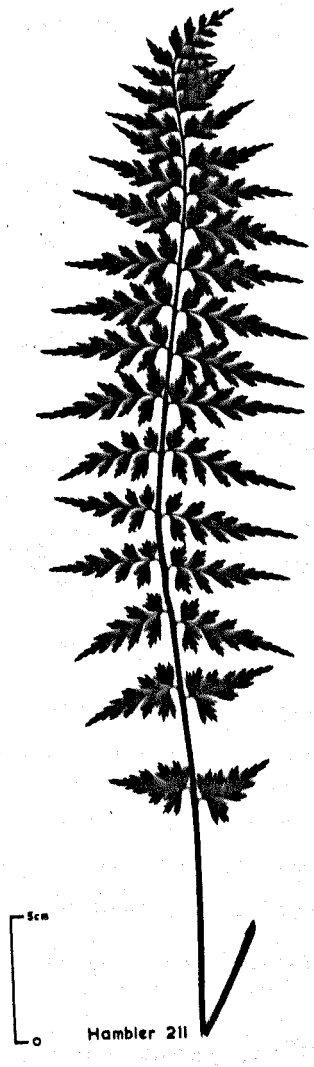
B485, Kericho, Kenya.
(terrestial)

(wild collections)



Kenya.
E. Africa.

Fig. 38.

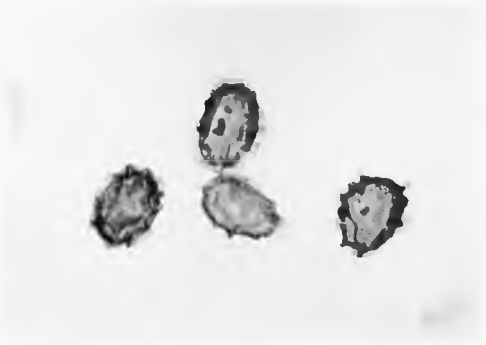


Nigeria.
W. Africa.

Fig. 39

Fronds from cultivated plants.

OCTOPLOID



a)

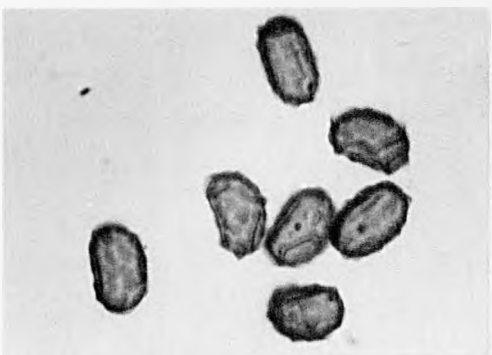
B263, Cape Peninsula,
South Africa.
(terrestial)

b)

B214, Transvaal,
South Africa.
(epiphytic)

c)

B485, Kericho,
Kenya.
(terrestial)



d)

B484, Kericho,
Kenya.
(epiphytic)

Fig. 40.

Spores. X 250.

Fig. 41. Distribution map for octoploid A. aethiopicum compiled from live and herbarium material.

(compare with tetraploid figs. 25, 30 and dodecaploid fig. 53)

Fig. 42. Octoploid A. aethiopicum growing among boulders, partially shaded by trees, in Window Gorge, Cape Peninsula. (B263 before collection)

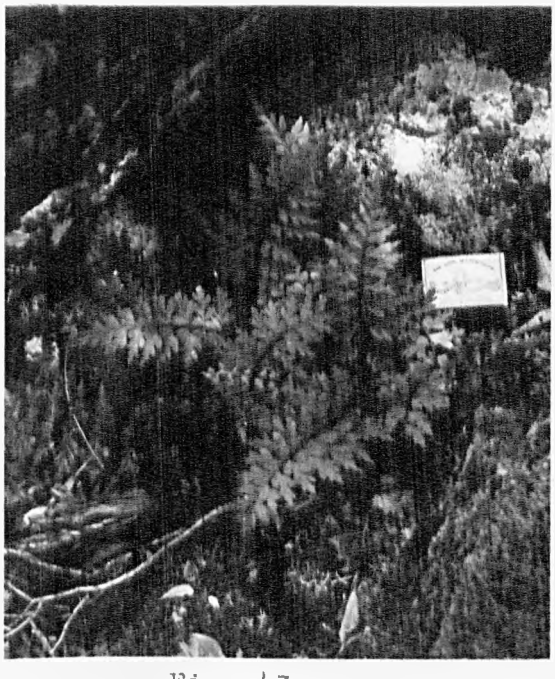


Fig. 43
Octoploid A. aethiopicum at Bains Kloof, Wellington Div., Cape Prov. Growing on partially shaded rocks by the roadside.

Fig. 44.
An octoploid plant (B115) epiphytic near the base of a tree trunk in the Kologha Forest, Stutterheim Div., Cape Province.

OCTOPLOID

A. demerkense Hier.

Fig. 45. Silhouette of a typical plant of A. demerkense Hier. from Mt. Kilimanjaro. X1/3.

Fig. 46. A frond from B392 (Mt. Kilimanjaro) showing a long stipe. X1/3.

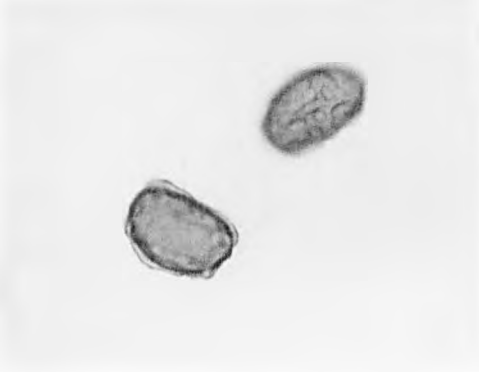


Fig. 47. Spores from B379. X250.

OCTOPLOID

A. demerkense Hier.

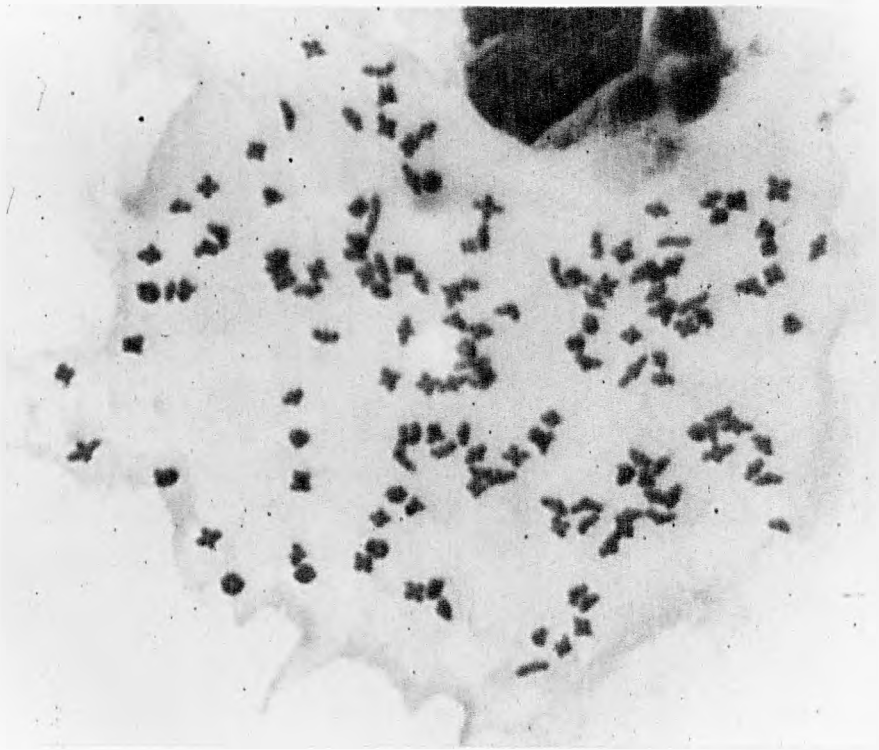


Fig. 48. Meiosis showing 144 bivalents in B379 from Mt, Kilimanjaro. X1000

Fig. 49.
B128, Transvaal,
South Africa.
(wild)

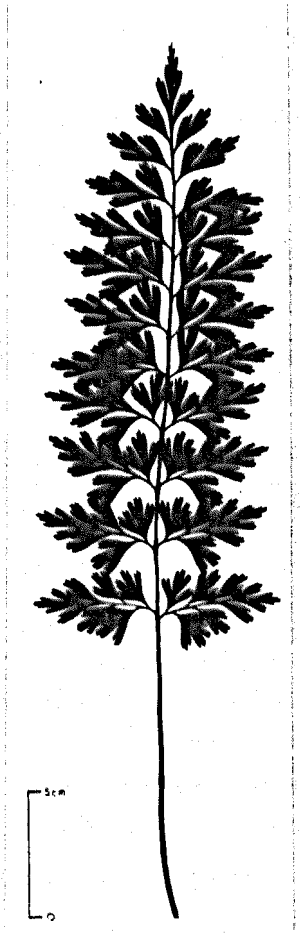


Fig. 50.
Kerr 137,
St. Helena.
(cultivated)

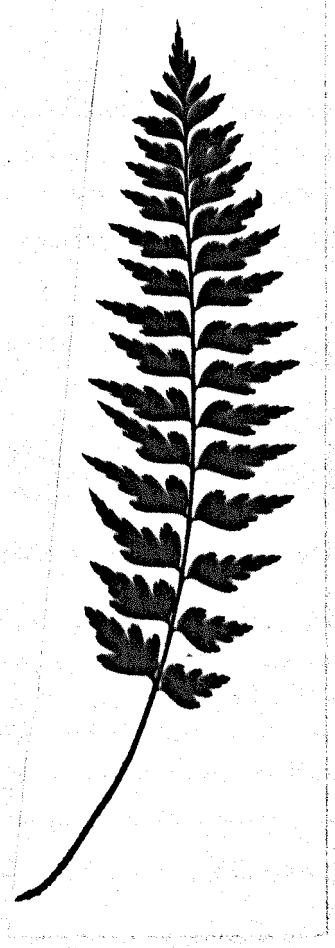
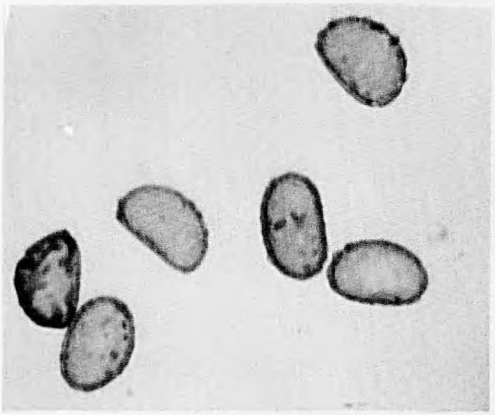


Fig. 51.
Manton,
Santa da Serra,
Madeira.
(cultivated)

Silhouettes of mature fronds from dodecaploid plants.
X1/3.

a) B128, Transvaal, South Africa.

b) Kerr 137, St. Helena.



c) Manton, Santa da Serra, Madeira.

Fig. 52. Spores. X250.

Fig. 53.

Map to show the distribution of the three dodecaploids.
Compiled from live and herbarium material.
(compare with tetraploids figs. 25, 30; and octoploids fig. 41)

Fig. 54.
(opposite page)

Hybrids between the tetraploid forms of A. aethiopicum.

Silhouettes of comparable pinnae (although those representing the hybrids tend to be from younger plants than those representing the parents) X 1/2.

The arrows point to the ♀ parent for each hybrid and the roman numerals correspond to the cross numbers used in the text.

ARTIFICIAL HYBRIDS

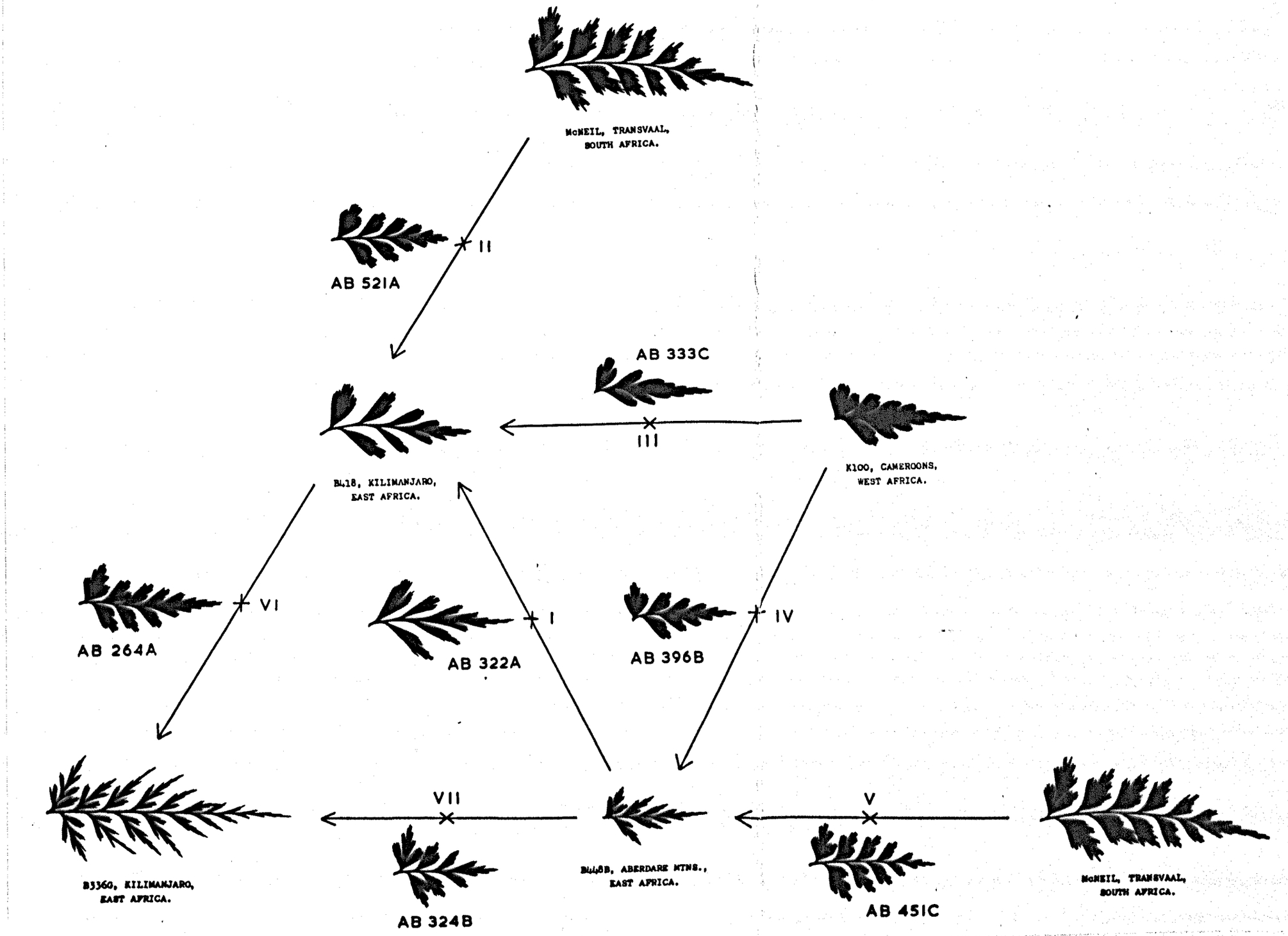


Fig. 54.

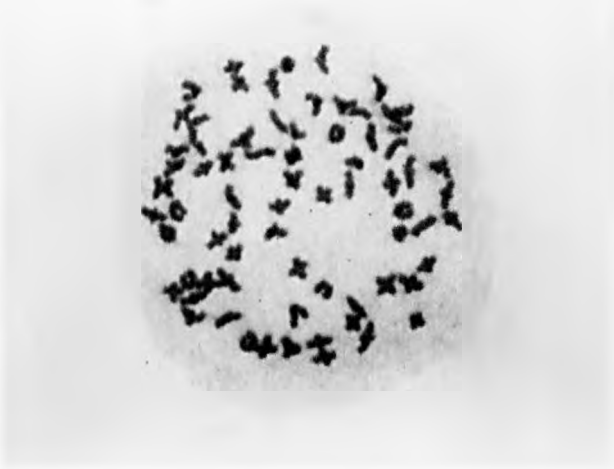


Fig 55.

Meiosis in the tetraploid hybrid AB 403B - A. aethiopicum B418 4x Kilimanjaro X A. aethiopicum var tripinnatum B 448B 4x Aberdares (cross i)

A cell showing 72 bivalents. X 1000.

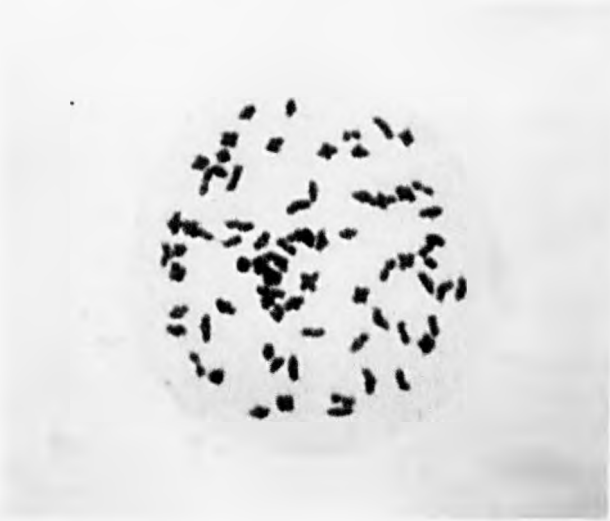


Fig. 56.

Meiosis in the tetraploid hybrid AB 521A - A. aethiopicum B418 4x Kilimanjaro X A. aethiopicum var tripinnatum McNeil s.n. 4x South Africa. (cross ii)

A cell showing 70 bivalents and 4 univalents. X 1000.

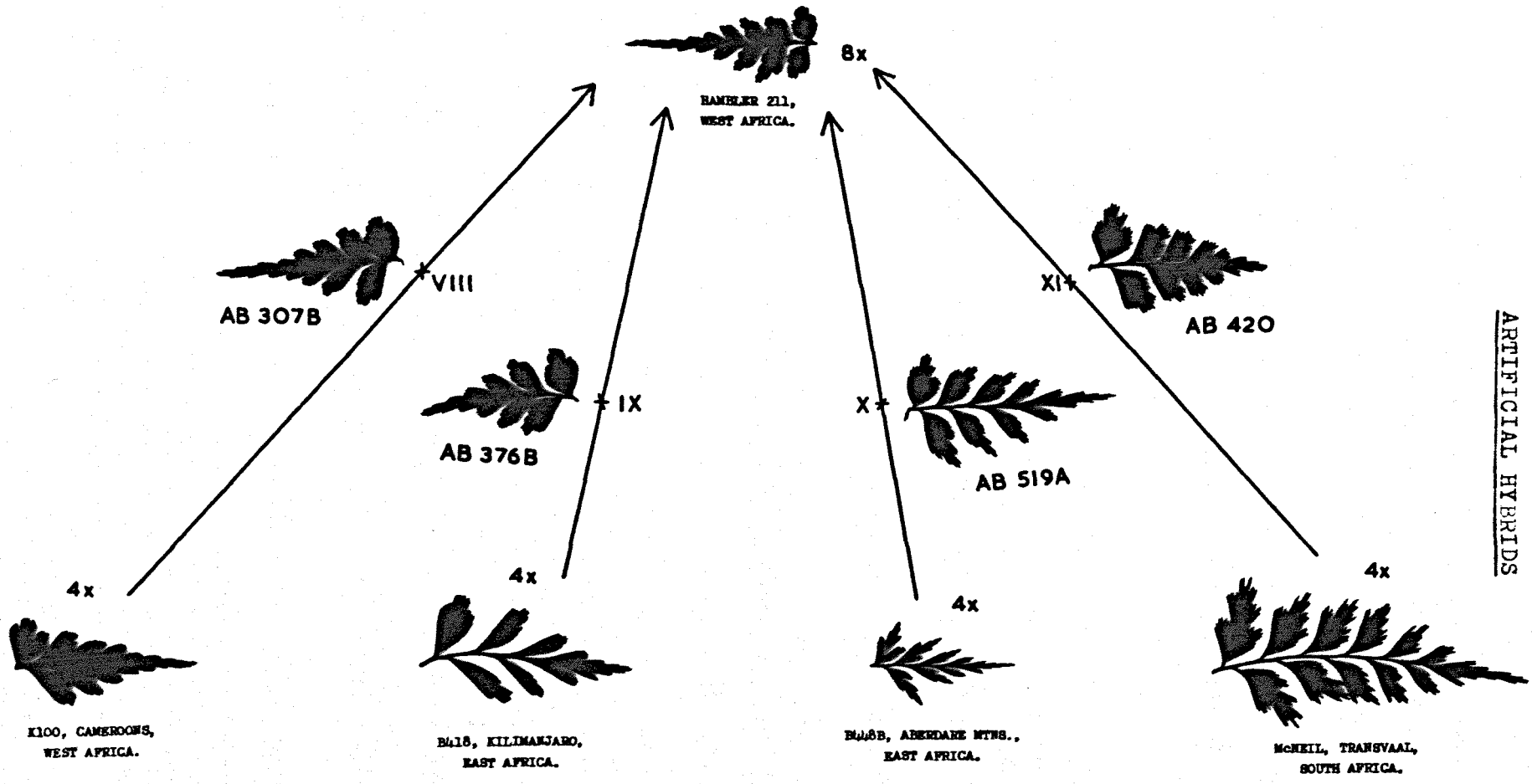


Fig. 57. Comparable pinnae from hexaploid hybrids synthesised between tetraploids and the octoploid Hambler 211 from West Africa. The arrows indicate the female parent and the roman numerals correspond to the number of the cross in the text. X $\frac{1}{2}$

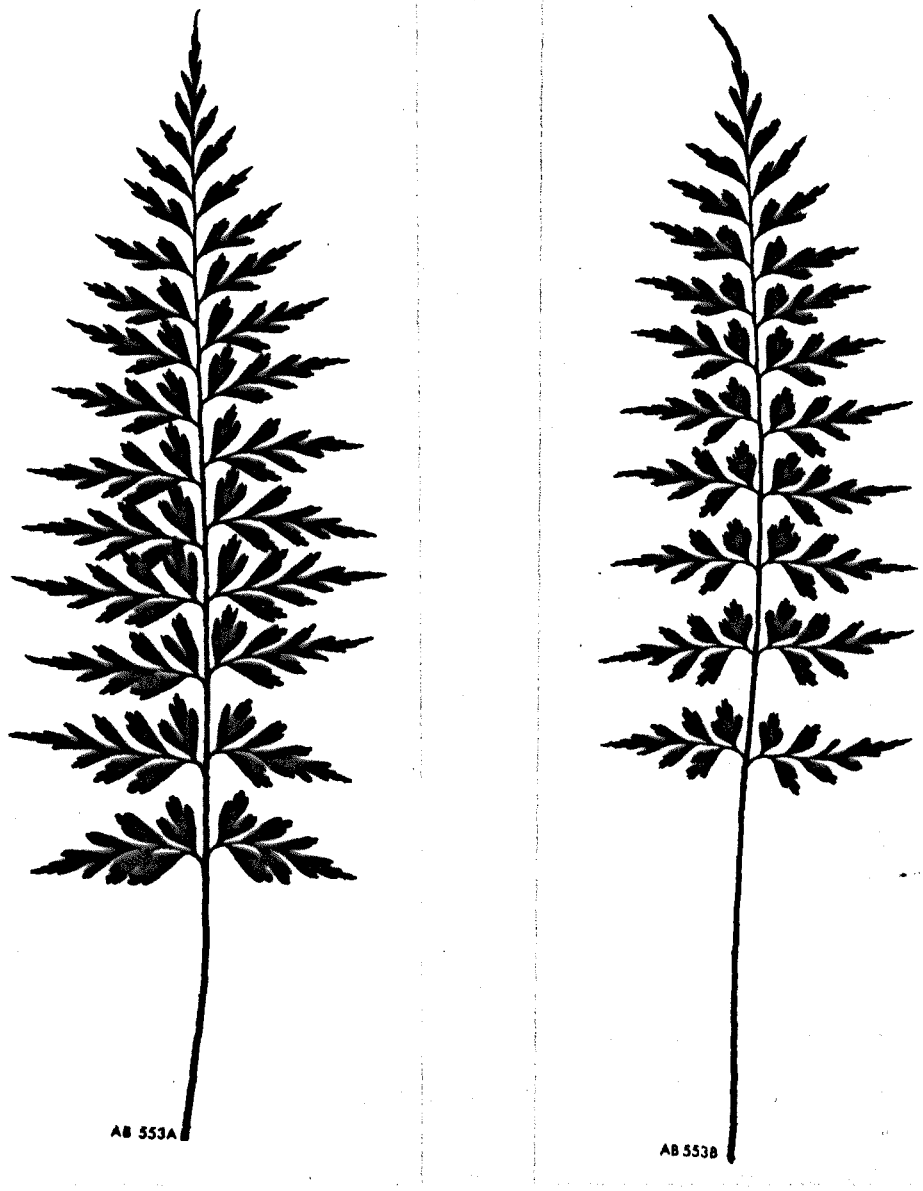


Fig. 58a.

Silhouettes of living fronds from the hexaploid (left) and the octoploid (right) hybrids which were synthesised between tetraploid A. aethiopicum B418 Mt. Kilimanjaro and octoploid A. aethiopicum B263 Cape S. Africa. (cross xvi) X 1/3

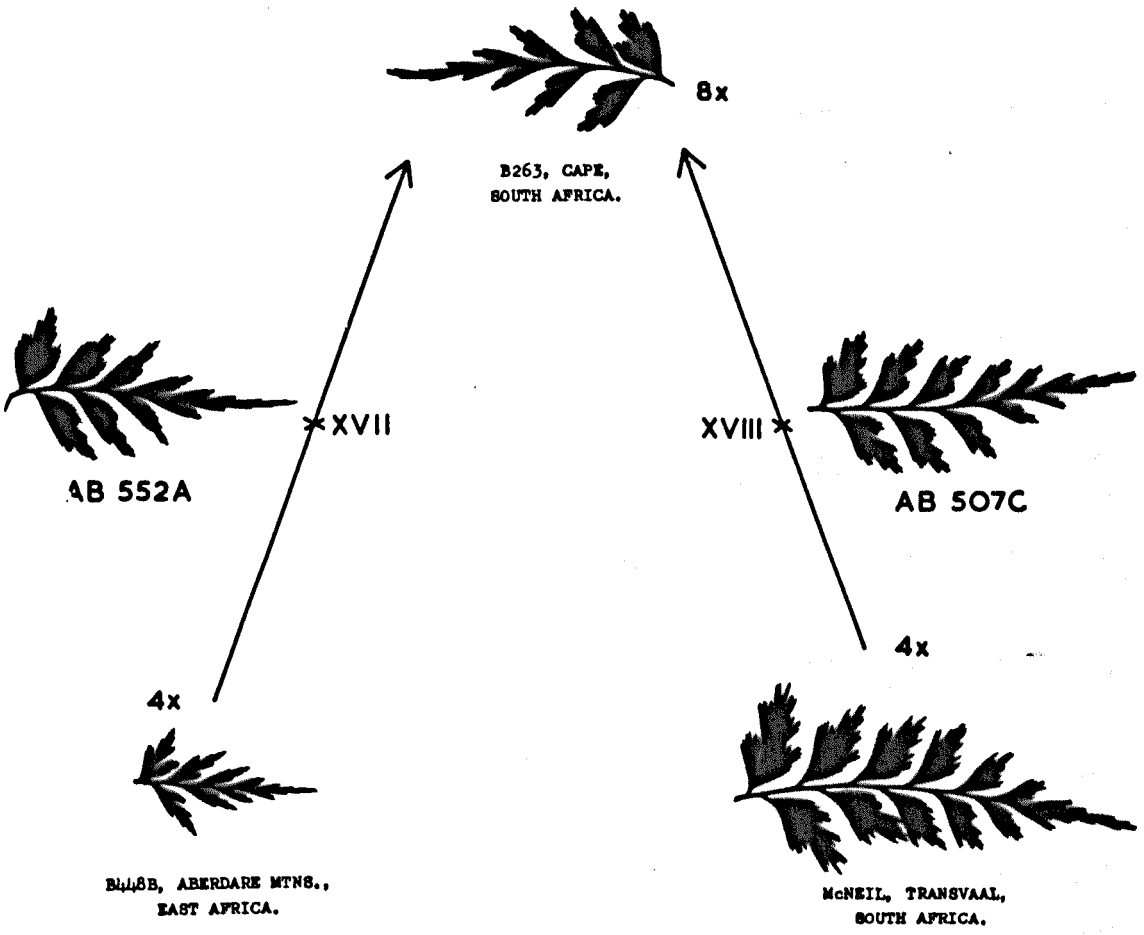
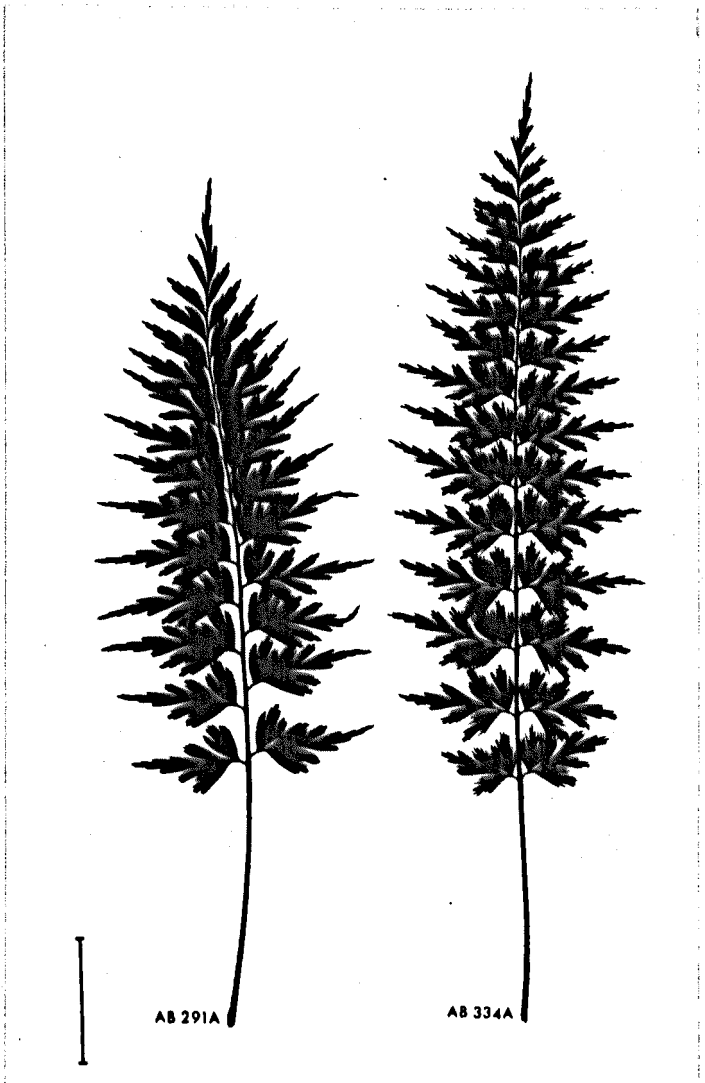


Fig. 58b.

Pinnae diagram for two hexaploid hybrids synthesised between octoploid A. aethiopicum B263 Cape S. Africa and tetraploid A. aethiopicum var tripinnatum B448B Aberdares E. Africa (cross xvii) and McNeil s.n. Transvaal S. Africa (cross xviii) X 1/2



a) (cross xix)

b) (cross xx)

Fig. 59.

Silhouettes of living fronds from two hybrids synthesised between A. demerkense Hier and tetraploid forms of A. aethiopicum. X 1/3.

a) Hexaploid hybrid.
♀ A. demerkense Hier B379 8x Kilimanjaro (fig. 45)
X ♂ A. aethiopicum B418 4x Kilimanjaro (fig. 26).

b) Octoploid hybrid.
♀ A. demerkense Hier B379 8x Kilimanjaro (fig. 45)
X ♂ A. aethiopicum var tripinnatum Baker B366G 4x Kilimanjaro (fig. 20).

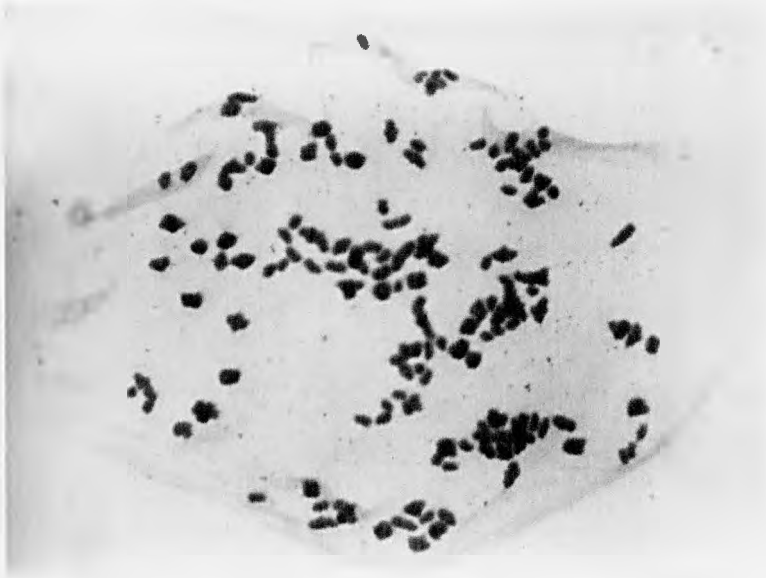


Fig. 60a. Meiosis in the hexaploid hybrid AB 127 between A. aethiopicum Hambler 211 8x W. Africa and A. aethiopicum var tripinnatum McNeil s.n. 4x S. Africa. (cross xi) X 1000.

Fig. 60b. Explanatory diagram for fig. 60a above showing 71 associations (solid) and 68 univalents (outlined). X 1500.

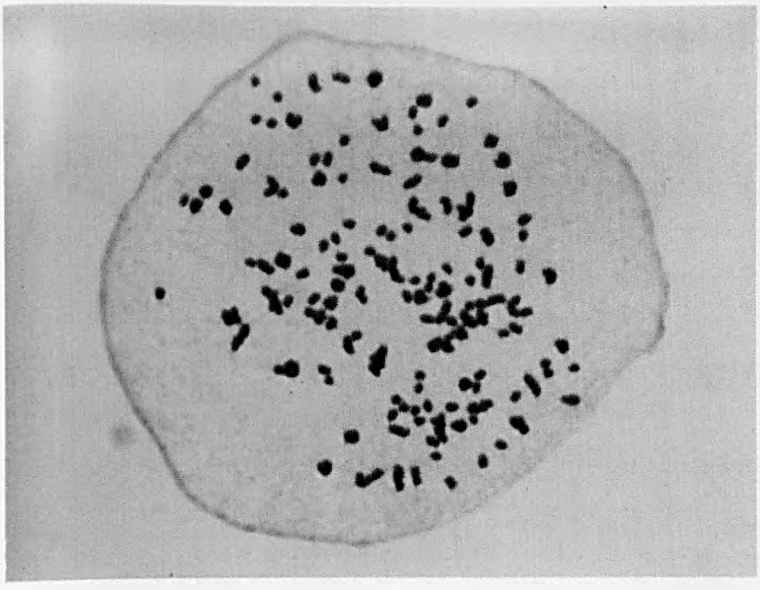


Fig. 61a. Meiosis in the hexaploid hybrid AB 223 - A. aethiopicum 8x Kenya X A. aethiopicum K100 4x Cameroons. (cross xii) X 1000.

Fig. 61b. Explanatory diagram for fig. 61a above showing 62 chromosome associations (solid) and 82 univalents (outlined). X 1500.

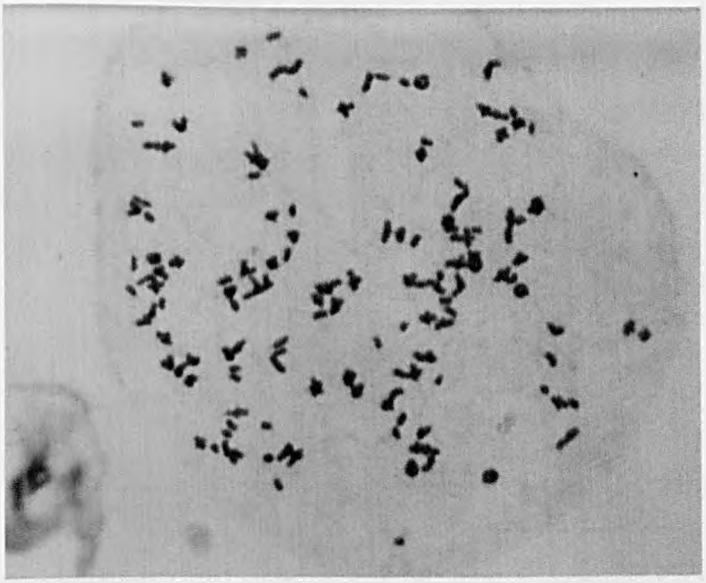


Fig. 62a. Meiosis in the hexaploid hybrid AB 7 - A. aethiopicum 8x Kenya X A. aethiopicum var tripinnatum McNeil s.n. 4x South Africa. (cross xiv) X 1000.

Fig. 62b. Explanatory diagram for fig. 62b above showing 74 associations and 57 univalents. X 1500.

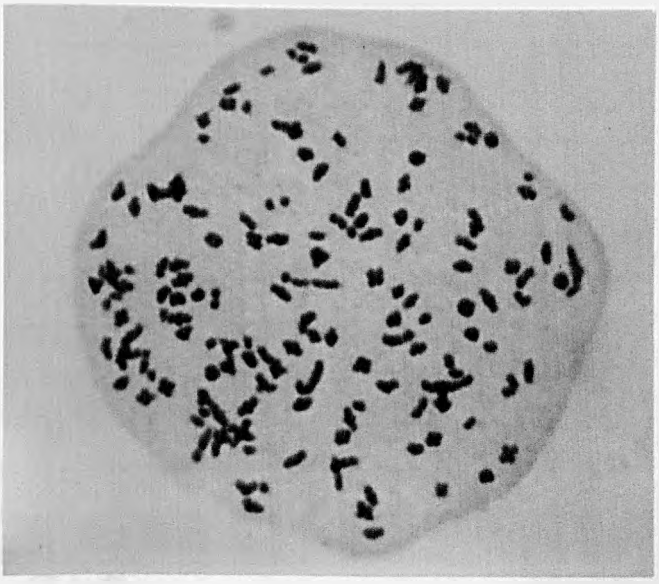
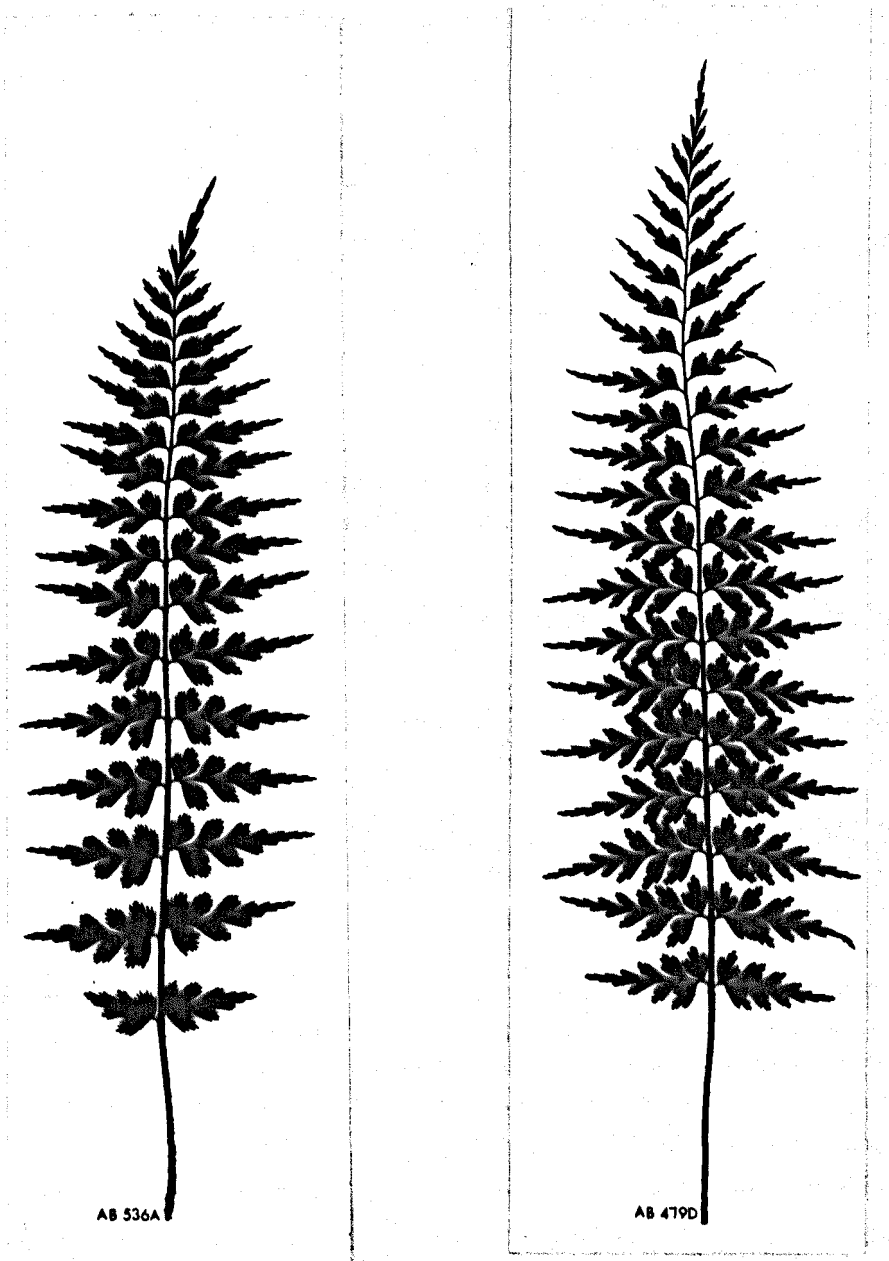


Fig. 63a. Meiosis in the octoploid hybrid AB 553B - A. aethiopicum B263 8x Cape X A. aethiopicum B418 4x Kilimanjaro. (cross xvi) X 1000.

Fig. 63b. Explanatory diagram for fig. 63a above showing 116 associations and 50 univalents. X 1500.



a)
(cross xxi)

b)
(cross xxii)

Fig. 64.

Silhouettes of frond from two octoploid hybrids synthesised between octoploid members of A. aethiopicum (Burm) Bech. X 1/3.

a) ♀ Hambler 211 8x W. Africa (fig. 39)
X ♂ 8x Kenya (fig. 38).

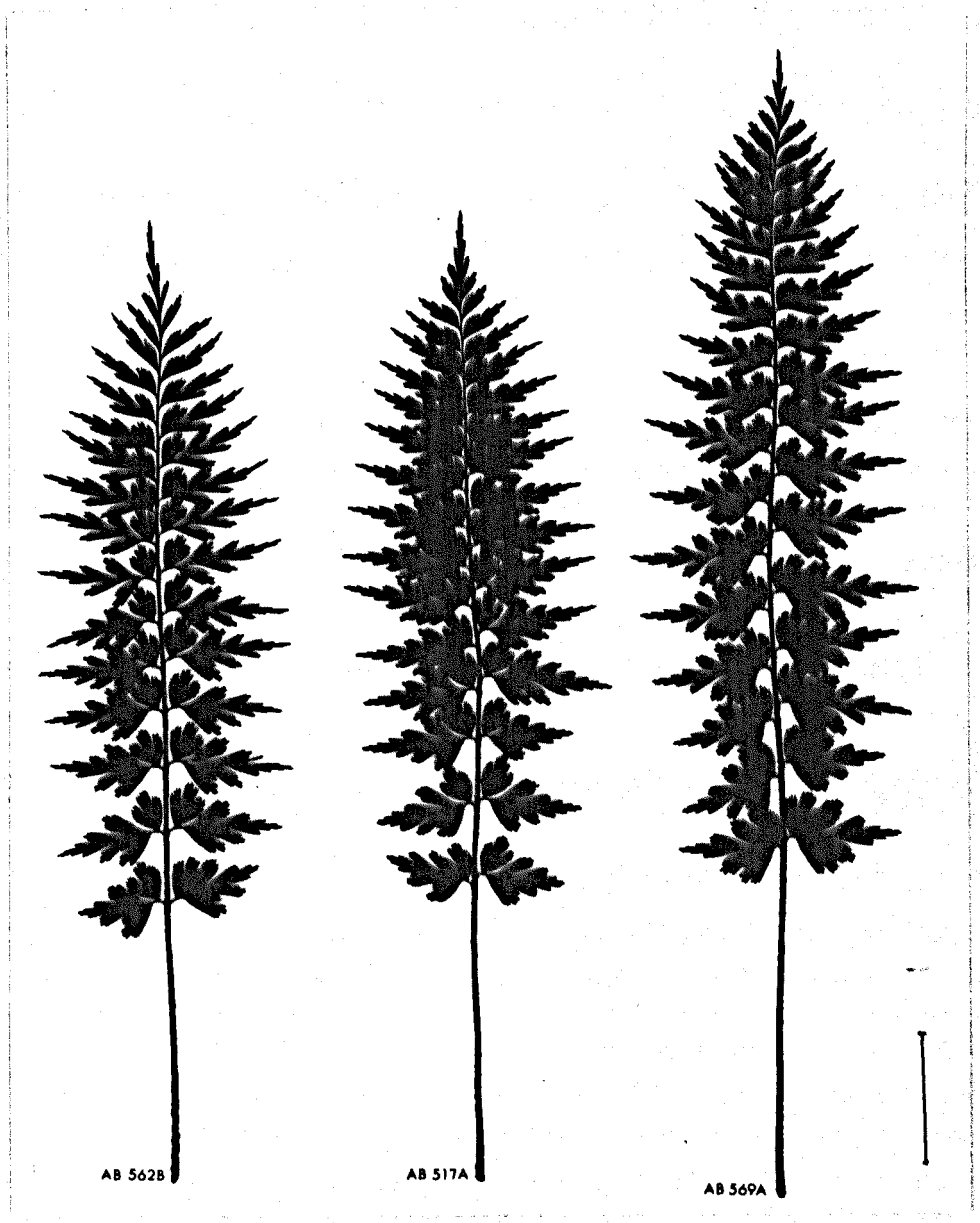
b) ♀ Hambler 211 8x W. Africa (fig. 39)
X ♂ B263 8x Cape Peninsula (fig. 32).

FURTHER EXPLANATION FOR FIG. 65. (opposite)

a) ♀ A. demerkense Hier. B379 8x Kilimanjaro (fig. 45)
X ♂ A. aethiopicum (Burm) Bech. B263 8x Cape (fig. 32).

b) ♀ A. demerkense Hier. B379 8x Kilimanjaro (fig. 45)
X ♂ A. aethiopicum (Burm) Bech. Schelpe 4281 8x Knysna S. Africa (fig. 34).

c) ♀ A. demerkense Hier. B379 8x Kilimanjaro (fig. 45)
X ♂ A. aethiopicum (Burm) Bech. Hambler 211 8x W. Africa (fig. 39).



a) (cross xxvi)

b) (cross xxv)

c) (cross xxiv)

Fig. 65.

Silhouettes of living fronds from octoploid hybrids synthesised between A. demerkense Hier. and octoploid A. aethiopicum (Burm) Bech.

X 1/3.

For parentage of hybrids see opposite page.

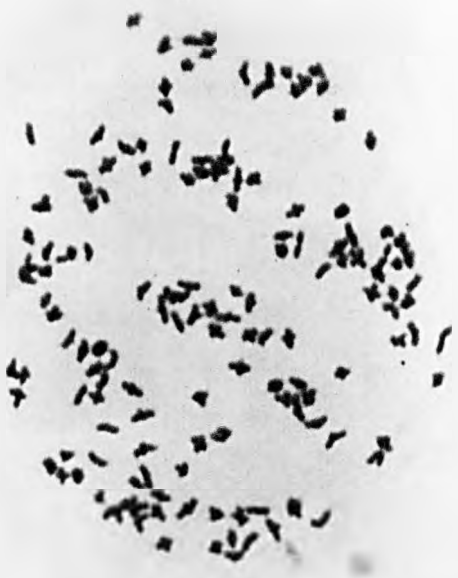


Fig. 66.

Meiosis in the octoploid hybrid AB 536A - A. aethiopicum Hambler 211 8x W. Africa X A. aethiopicum 8x Kenya. (cross xxi)

A cell showing 143 bivalents and 2 univalents. X 1000.

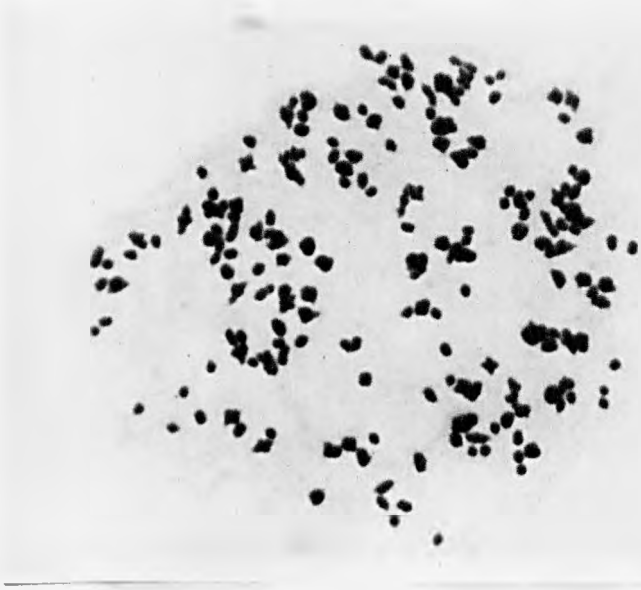
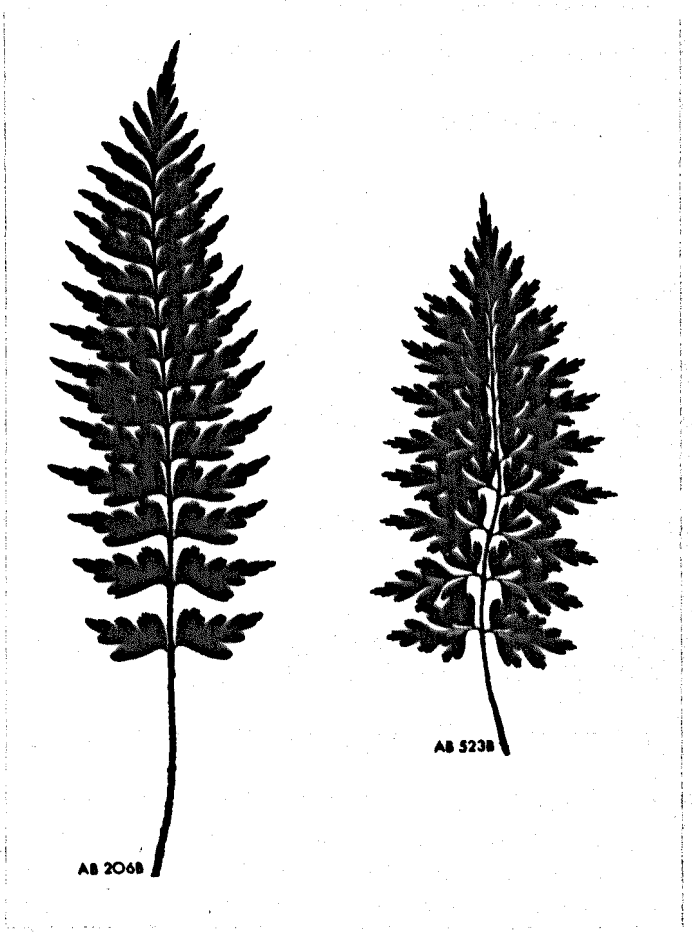


Fig. 67a. Meiosis in the octoploid hybrid AB 570A - *A. demerkense* B379 8x Kilimanjaro X *A. aethiopicum* Hambler 211 8x W. Africa. (cross xxiv) X 1000.

Fig. 67b. Explanatory diagram for fig. 67a above showing 99 chromosome associations and 87 univalents. X 1500.



a)
(cross xxvii)

b)
(cross xxviii)

Fig. 68.

Silhouettes of living fronds from two octoploid hybrids synthesised between the dodecaploid and tetraploid cytotypes. X 1/3.

a) ♀ A. aethiopicum Manton s.n. 12x Madeira (fig. 51)
X ♂ A. aethiopicum K100 4x Cameroons (fig. 29)

b) ♀ A. aethiopicum B128 12x S. Africa (fig.49) X ♂ A. aethiopicum var tripinnatum McNeil s.n. 4x S. Africa (fig. 14)

Fig. 69a. Meiosis in the octoploid hybrid AB 206B between A. aethiopicum 12x Madeira and A. aethiopicum K100 4x Cameroons. (cross xxvii) X 1000.

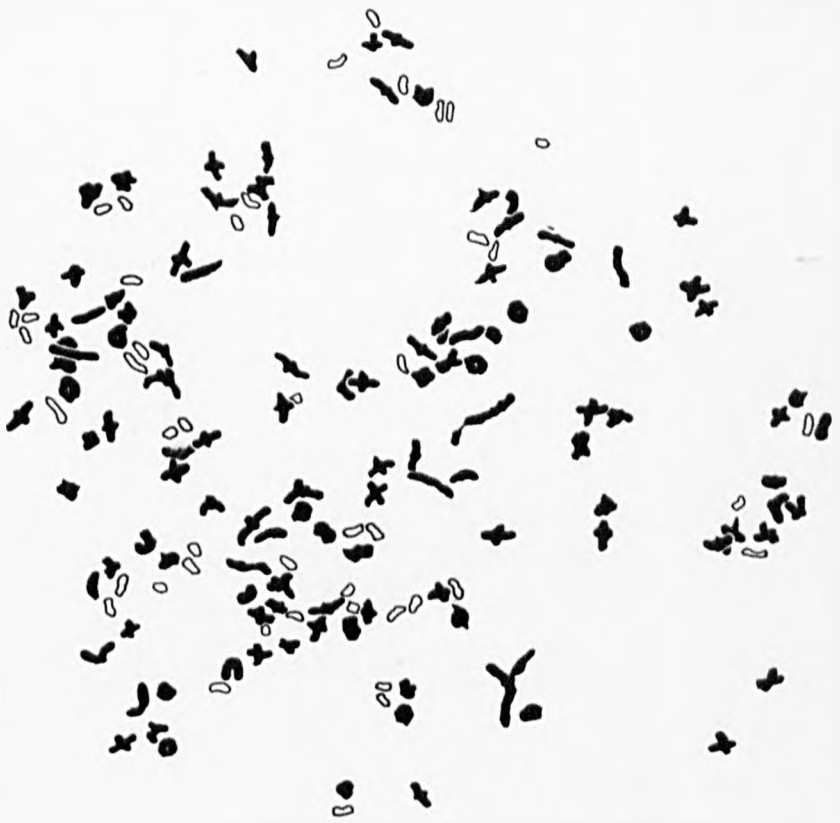


Fig. 69b. Explanatory diagram for fig. 69a above showing 119 associations and 45 univalents. X 1500.

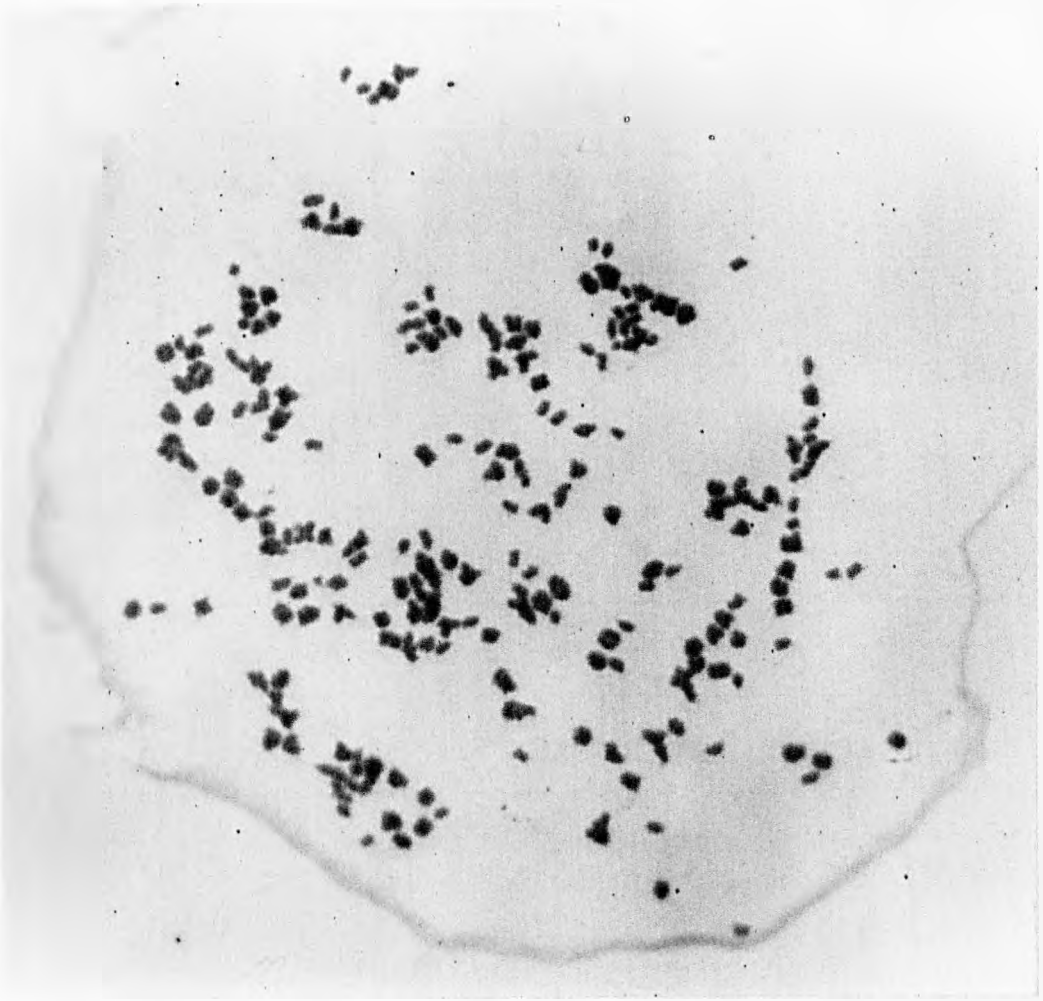
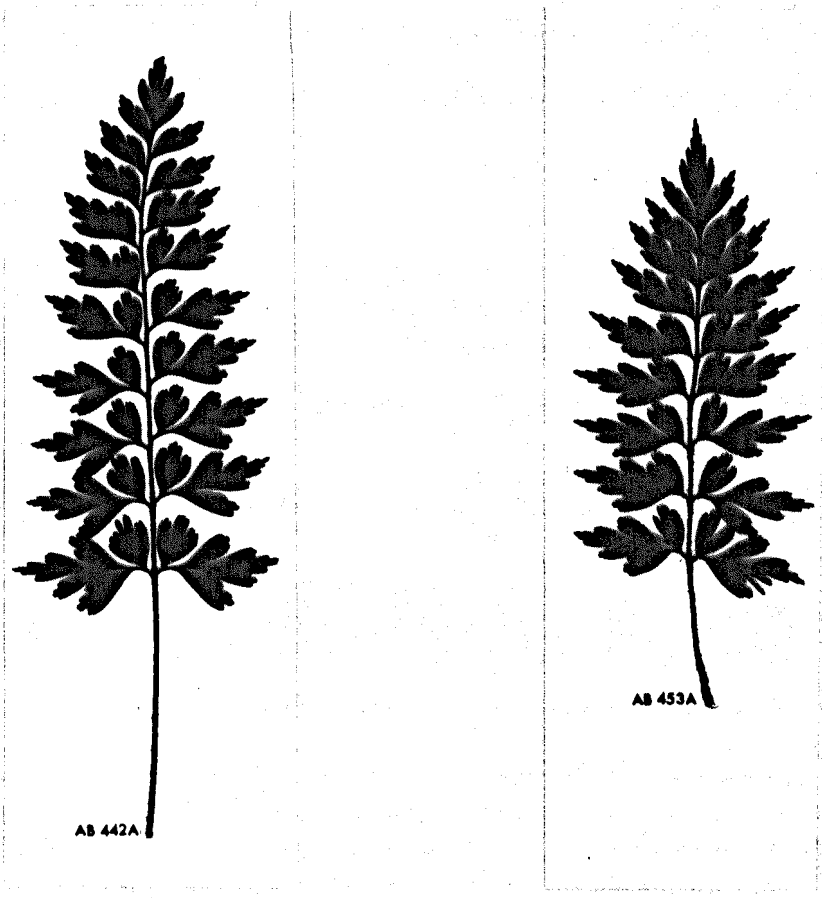


Fig. 70. Meiosis in the decaploid hybrid AB 259A - *A. aethiopicum* 12x Madeira X *A. aethiopicum* B418 4x Kilimanjaro. (hybrid xxxi, p. 79)
A cell showing approximately 120 chromosome associations and 101 univalents. X 1000.



a)
(cross xxxiii)

b)
(cross xxxiv)

Fig. 71.

Silhouettes of living fronds from two dodecaploid hybrids. X 1/3.

a) ♀ A. aethiopicum Kerr 137 12x St. Helena (fig. 50)
X ♂ A. aethiopicum Manton s.n. 12x Madeira (fig 51).

b) ♀ A. aethiopicum B128 12x S. Africa (fig. 49)
X ♂ A. aethiopicum Manton s.n. 12x Madeira (fig. 51).

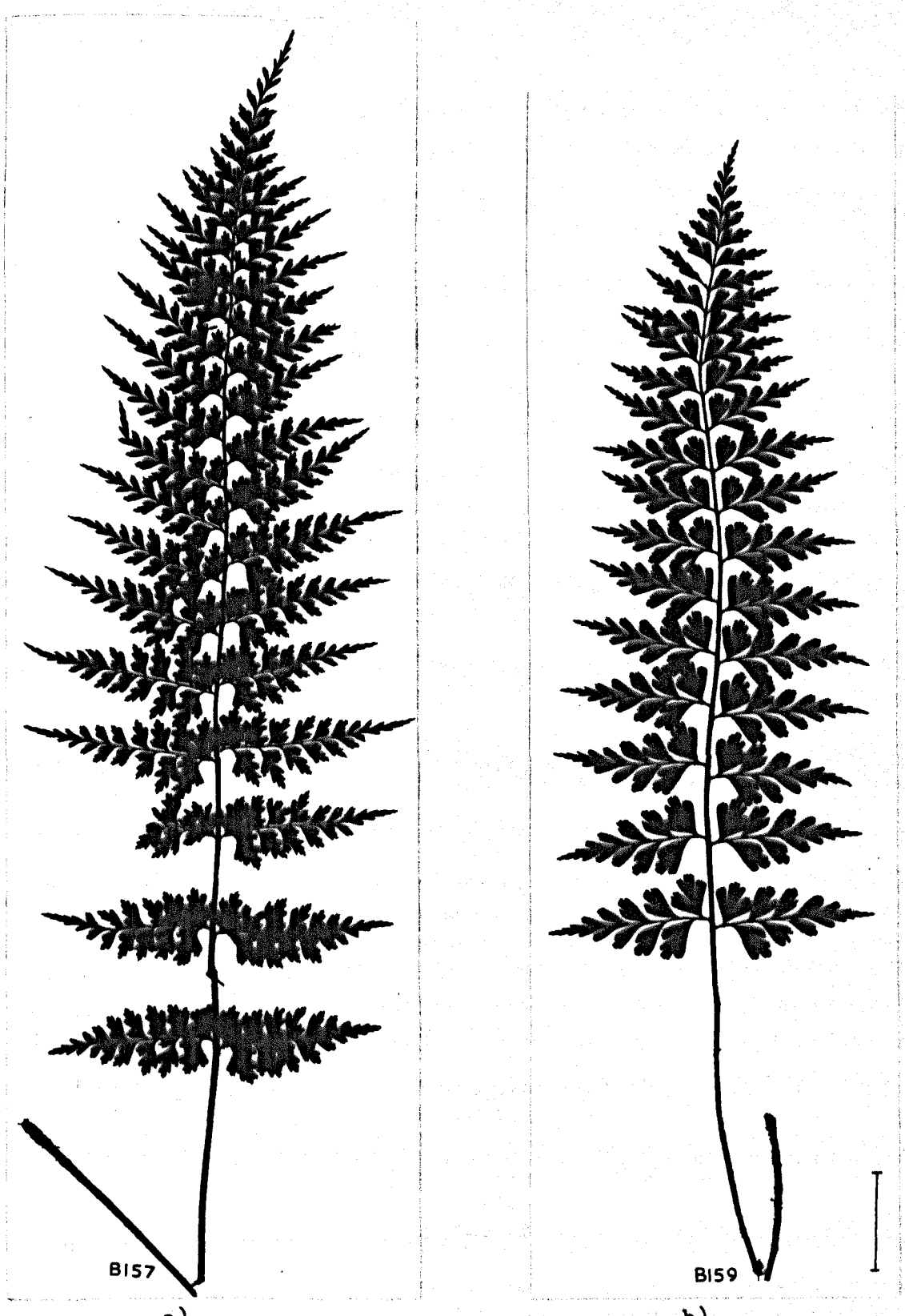


Fig. 72. Silhouettes of fronds collected in the wild of the tetraploid A. aethiopicum var tripinnatum Baker B157 (a) and the sterile hexaploid plant B 159 (b) from the Ceylon Forest Reserve, Transvaal, South Africa. X 1/3.

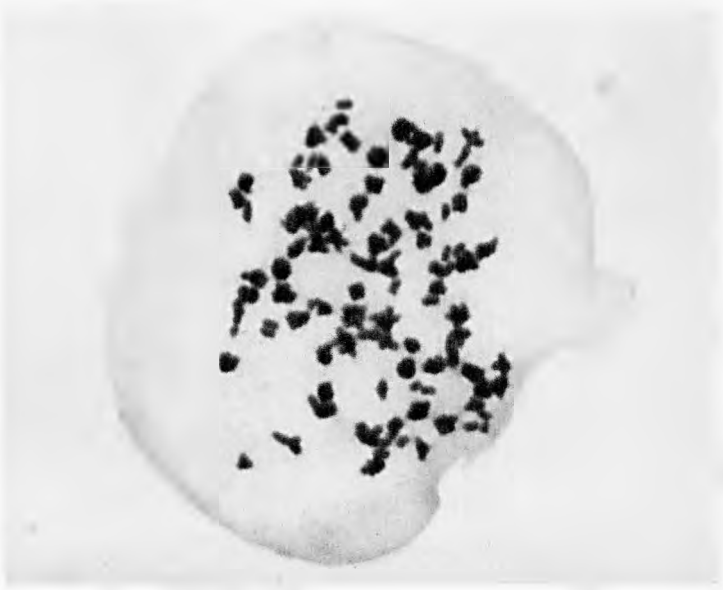


Fig. 73.

Meiosis in the sterile hexaploid plant B235 from Kowyn's Pass, nr. Graskop, Transvaal, South Africa. X 1000

The cell shows approximately 71 chromosome associations and 25 univalents. Many of the associations are multivalent (see top right) which accounts for the low number of unpaired chromosomes.

Fig. 74. The two natural hexaploid hybrids and their putative parents from Kericho, Kenya. Comparable pinnae - natural size.

Explanation for Fig. 75.

Meiosis in apogamous A. aethiopicum. Sections of sporangia from Braithwaite 228 (1-4, 6) and Nash 183 (5).

All preparations stained in Heidenhain's haematoxylin and photographed at a magnification of X 500.

1. Prophase.
2. Diakinesis.
3. The first meiotic metaphase. Note the exceedingly irregular appearance.
4. Restitution representing interphase.
5. The second meiotic division with only one spindle.
6. Diads.

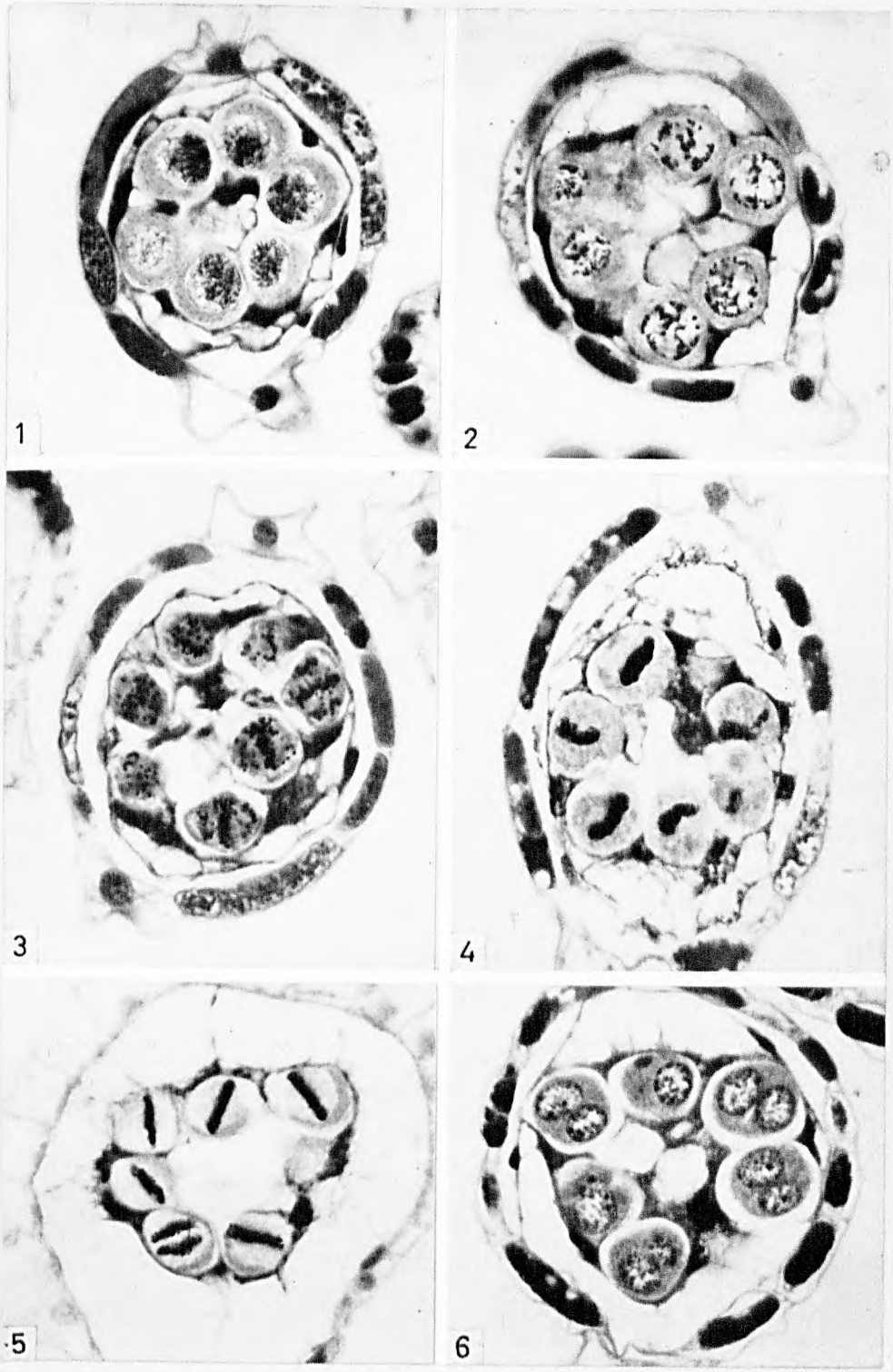


Fig. 75.

Explanation for Fig. 76.

Meiosis in apogamous *A. aethiopicum*. Detail from sections of sporangia from Braithwaite 228.
All preparations stained in Heidenhain's haematoxylin and photographed at a magnification of X 1000.

7. Diakinesis showing univalents from the same sporangium as fig. 75:2.

8. The first irregular metaphase showing highly contracted univalents scattered over the spindle area. The same section as fig. 75:3.

9. Cells showing nearly all the univalents lying in the equatorial region of the spindle.

10. Detail of restitution nuclei from the same sporangium as fig. 75:4. Traces of a former spindle may sometimes be observed as in the mother cell to the lower right.

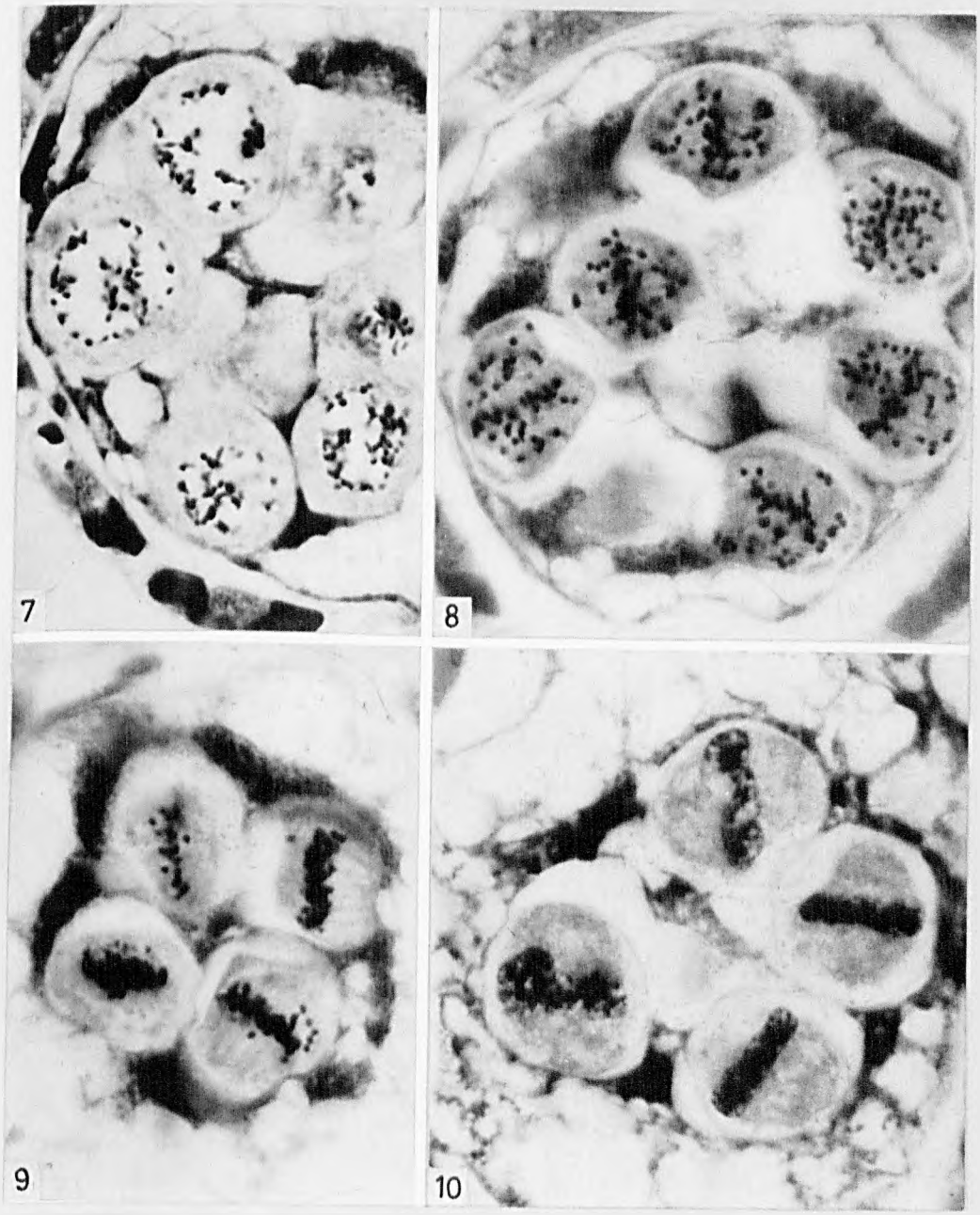
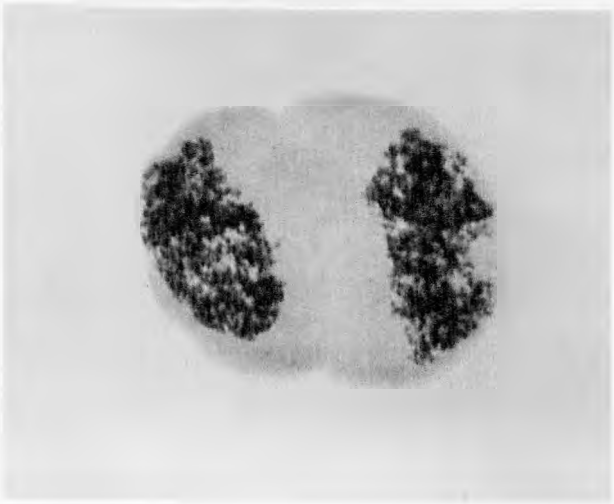
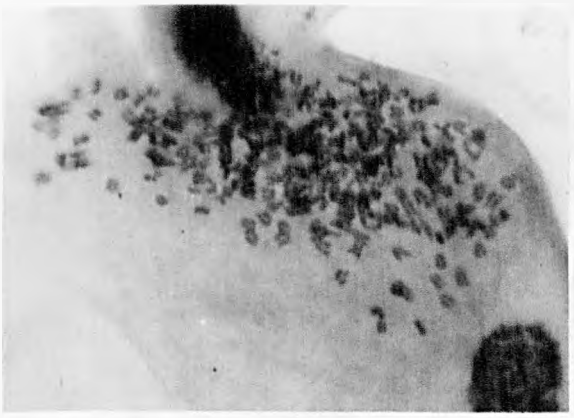


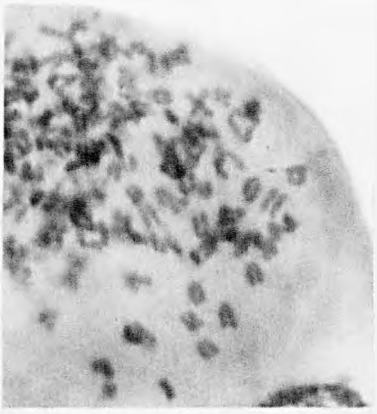
Fig. 76.



c)



a)



b)

Fig. 77.

Acetocarmine squash preparations of meiosis in apogamous A. aethiopicum.

a) The second meiotic metaphase from Nash 183 showing the univalents to be conspicuously double. X 1000.
b) shows detail of the split univalents from the same cell as a). X 1500.
c) A diad from B228. X 1000.

Fig. 78a. Meiosis in octoploid apogamous A. aethiopicum (Mitchell 88) from Dombashawa, nr. Salisbury, Southern Rhodesia.
Acetocarmine squash preparation. X 1000.

Fig. 78b. Explanatory diagram for fig. 78a above showing 288 univalents. X 2000.

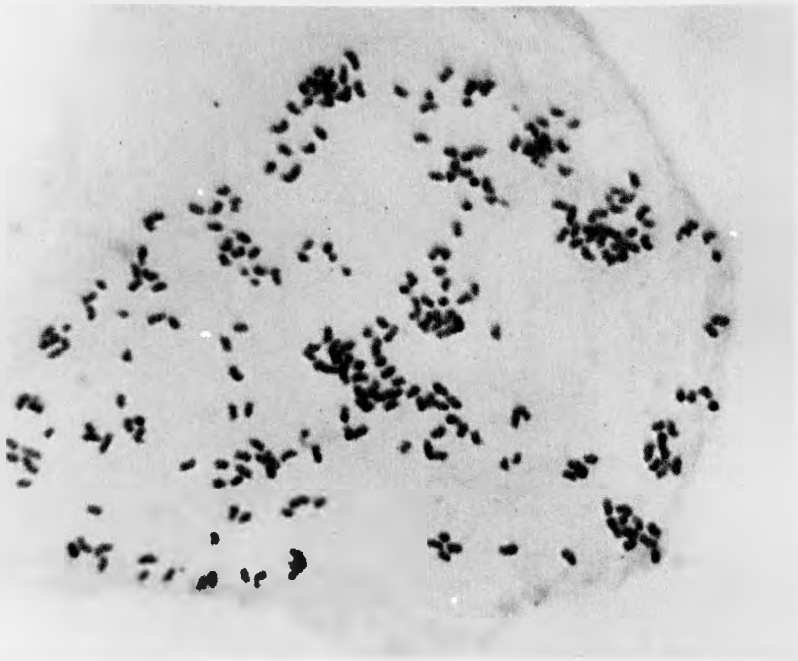


Fig. 79a. Diakinesis in octoploid apogamous A. aethiopicum (B228) from Pilgrim's Rest, Transvaal, South Africa. Acetocarmine squash preparation. X 1000.

Fig. 79b. Explanatory diagram for fig. 79a above showing 288 univalents. X 1500.

Fig. 80a. 'Meiosis' in apogamous A. aethiopicum. Diakinesis showing univalents in the decaploid cytotype B103A from Doringberg, nr. Conway, Cape Province, South Africa. X 1000.

Fig. 80b. Explanatory diagram for fig. 80a above showing 357 univalents. X 1500.

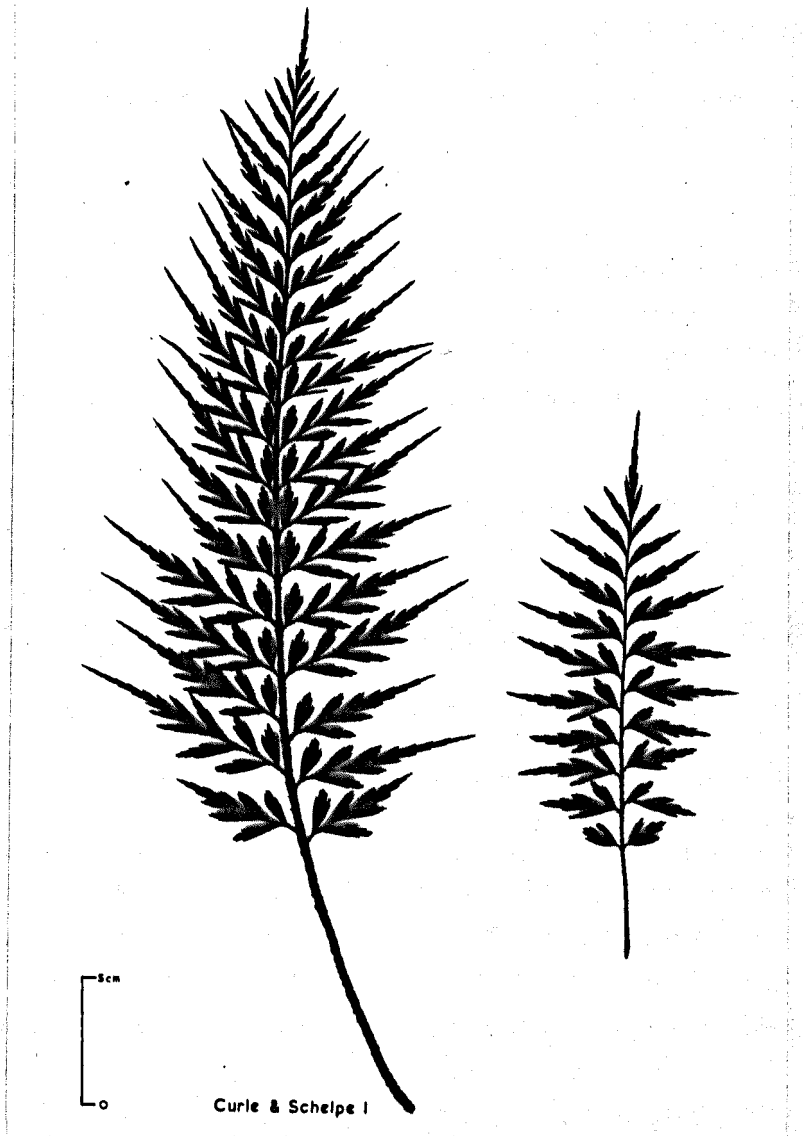


Fig. 81.

A. filare (Forsk) Alston from Ethiopia.

Silhouettes of two fresh fronds from the same plant in cultivation (Curle & Schelpe I). X 1/3.

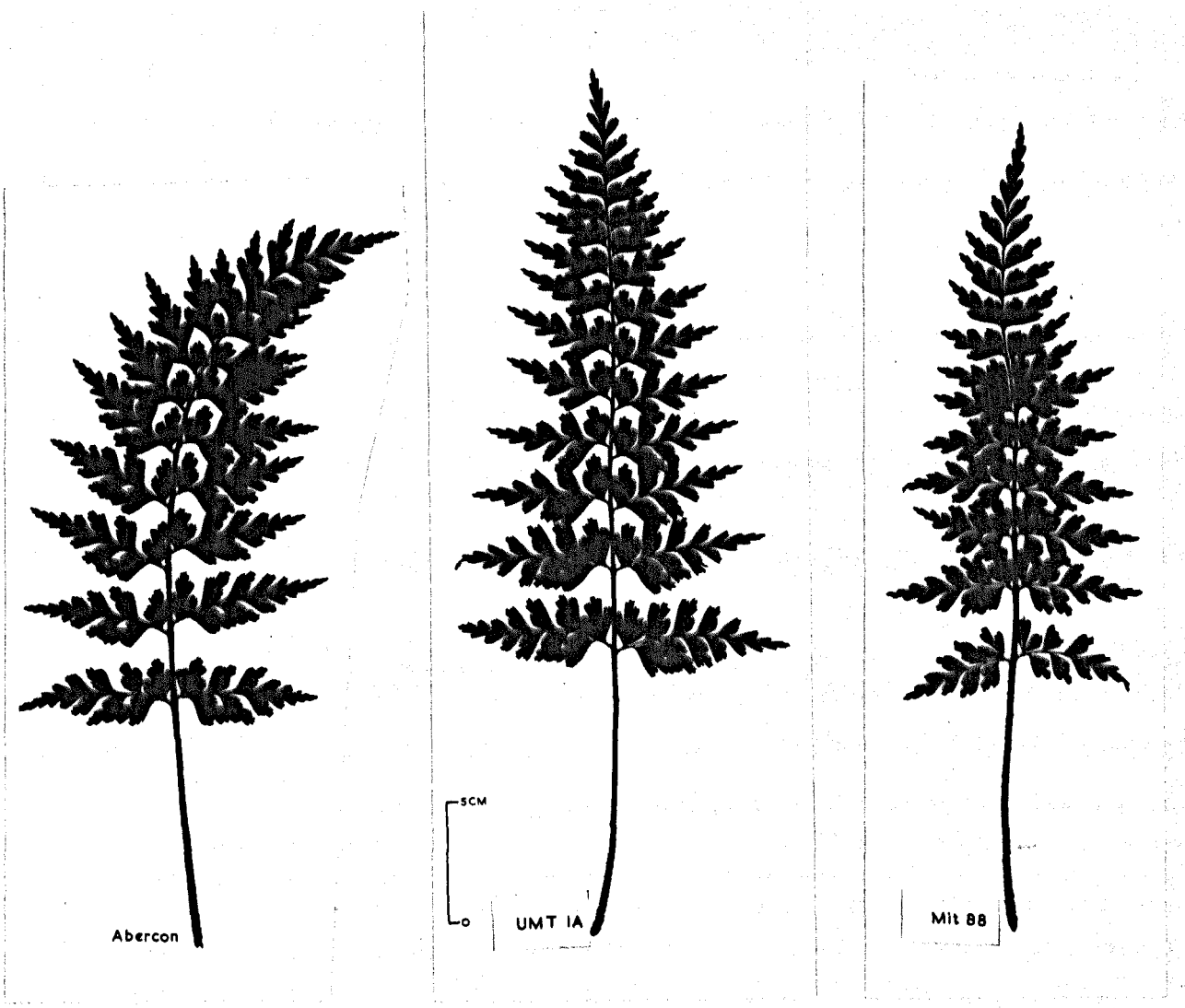


Fig. 82.

Apogamous A. aethiopicum from Northern and Southern Rhodesia.

Silhouettes of living frond from cultivated plants. X 1/3.

a) Nash 183, nr. Abercon, Northern Rhodesia.
b) Williams UMT. 1A, Umtali, Southern Rhodesia.
c) Mitchell 88, nr. Salisbury, Southern Rhodesia.

Further explanation for Fig. 83.

a) Braithwaite 228, Pilgrim's Rest, Transvaal.

b) Braithwaite 103B, Nr. Conway, Cape Province.

c) Braithwaite 222, Pilgrim's Rest, Transvaal.

d) Braithwaite 103A, Nr. Conway, Cape Province.

e) Garstfontein 'c', Garstfontein, Pretoria, Transvaal.
(collected by the National Herbarium, Pretoria)

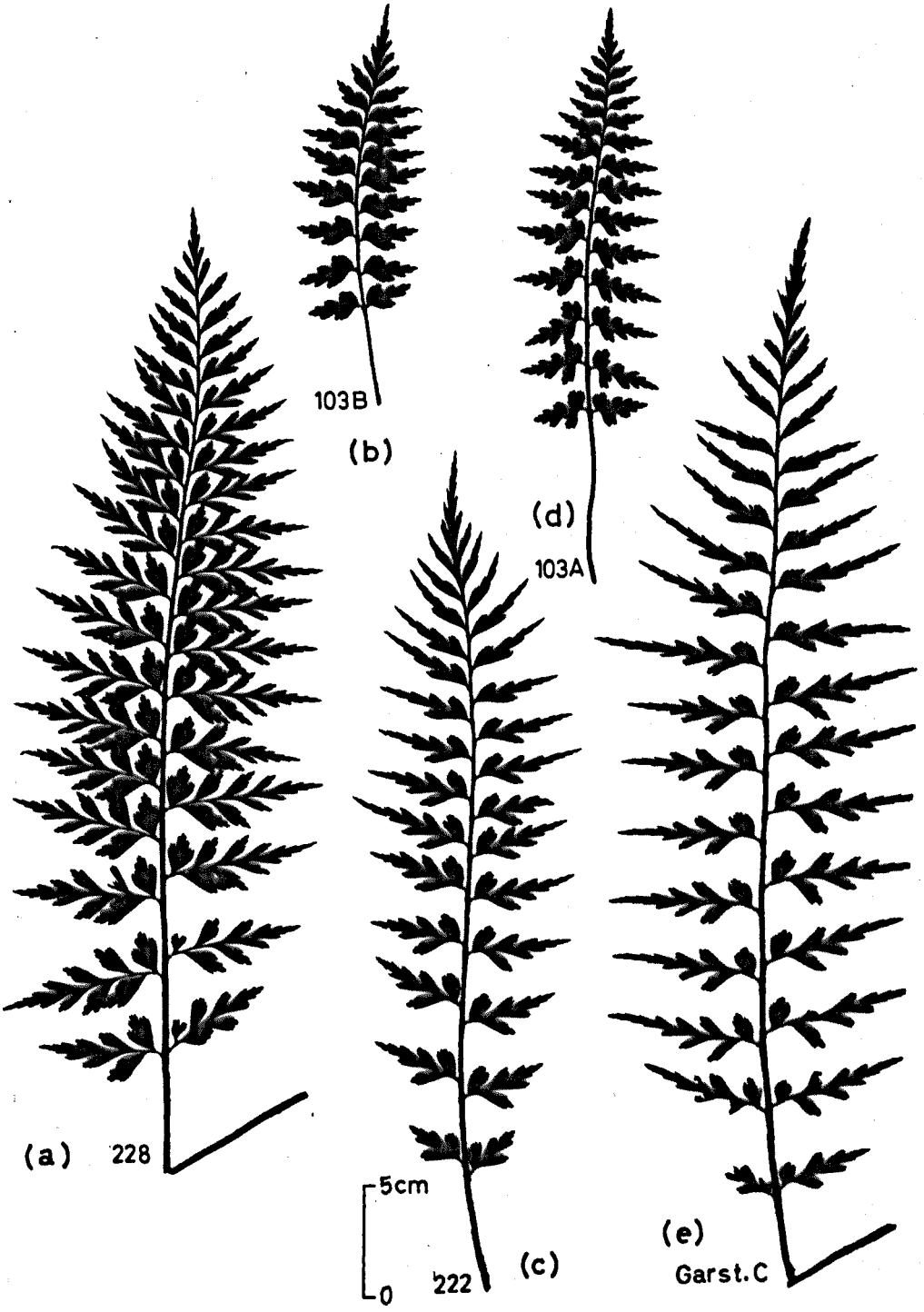
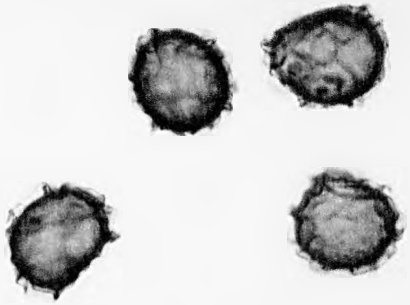


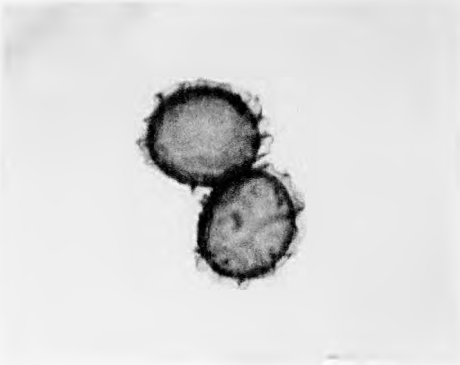
Fig. 83.

Apogamous A. aethiopicum from South Africa. Silhouettes of living fronds taken from plants of comparable ages in cultivation. For explanation of collectors numbers see page opposite. X 1/3.

a) A. filare (Forsk) Alston.
Group I.
Curle & Schelpe I. from
Ethiopia.



b) A. aethiopicum.
Group II.
Nash 183, Abercon,
Northern Rhodesia.



c) A. aethiopicum.
Group III.
B228, Transvaal,
South Africa.

Fig. 84.

Spores from apogamous plants. X 250.

(Compare with spores of sexual plants shown in figs. 28, 40, 52.)

Fig. 85.

Map compiled from herbarium material and fieldwork to show the general distribution of the apogamous forms of the A. aethiopicum complex in Africa.

The broken red line encloses Group II with Group I (A. filare (Forsk) Alston) to the north and Group III to the south.

FIGS. 86 - 87.

Distribution maps of apogamous and sexual members of the A. aethiopicum complex in southern Africa.

(OVER)

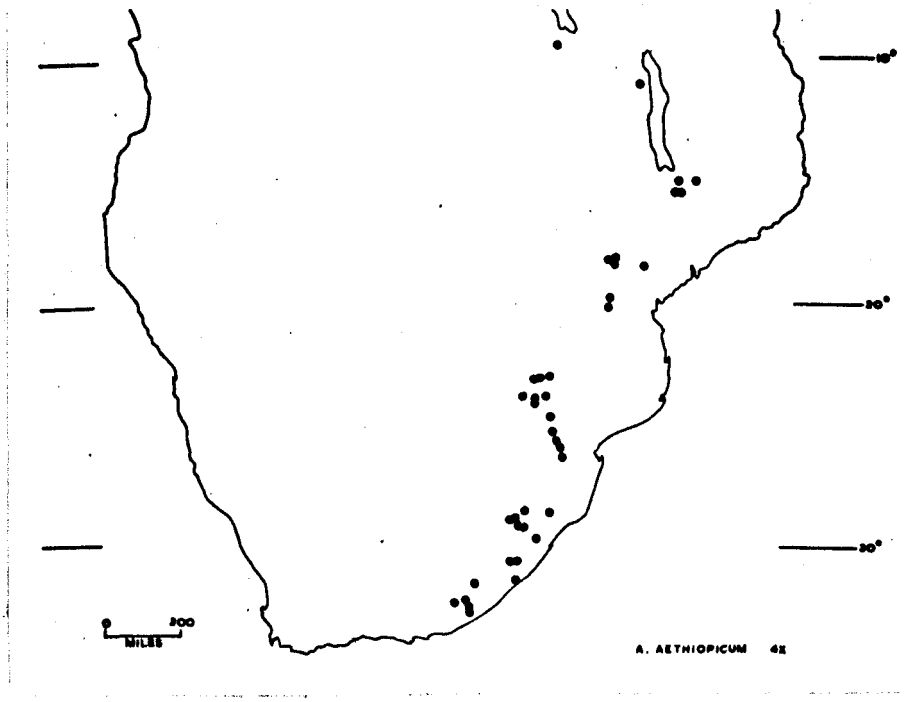


Fig. 86a. Map showing the distribution of tetraploid A. aethiopicum in southern Africa.

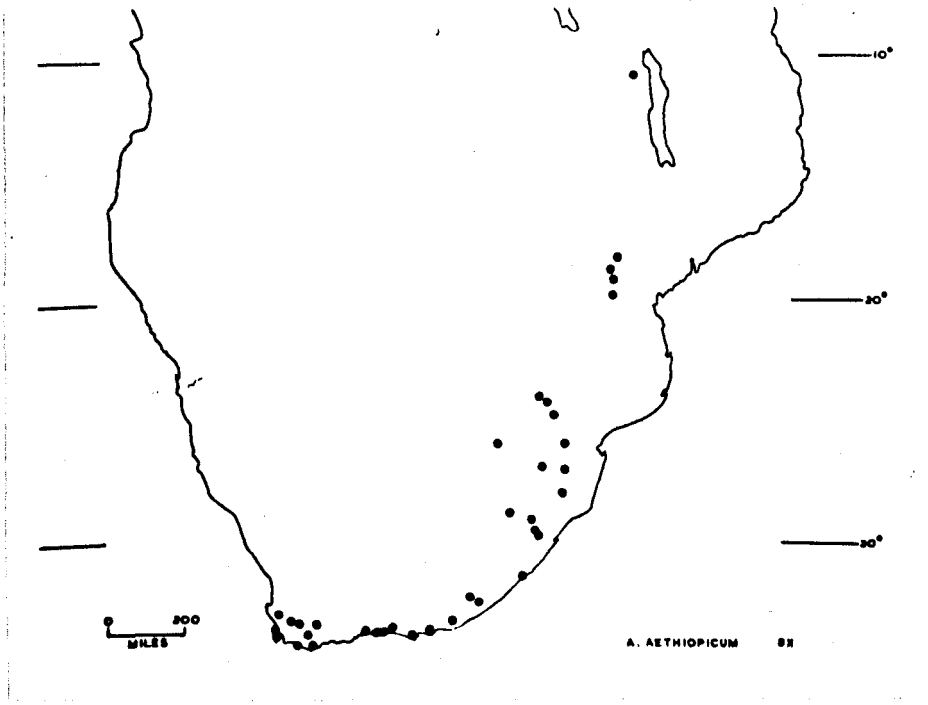


Fig. 86b. Map showing the distribution of sexual octoploid A. aethiopicum in southern Africa.

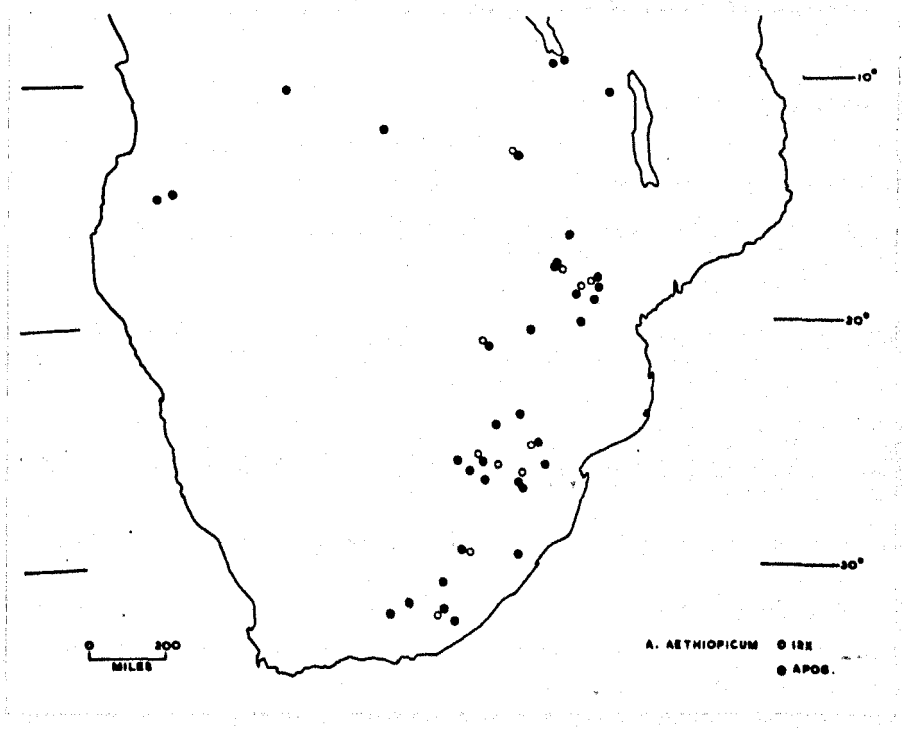


Fig 87.

Map to show the distribution of apogamous and sexual dodecaploid A. aethiopicum in southern Africa.

(Compare with figs 86a and 86 b opposite)